How early rearing conditions influence behaviour and survival of pheasants released into the wild?

Submitted by Mark Andrew Whiteside to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology in February 2015.

I certify that all material in the thesis which is not my own has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature:

ABSTRACT

Translocation programmes, particularly when using the release of a captive reared population, often fail in their efforts to create a self-sustaining population. High mortality after release is a key issue and often associated with behavioural, physiological and cognitive deficiencies between the released population and their wild counterparts. Mitigation of these deficiencies is essential for successful translocation programmes.

I showed that pheasants (*Phasianus colchicus*) that were reared in more naturalistic conditions early in life were better suited to the natural environment after they were released into the wild. Post release survival was improved with exposure to more naturalistic diets prior to release. We identified four mechanisms to explain this. Pheasants reared with more naturalistic diets: 1) foraged for less time and had a higher likelihood of performing vigilance behaviours; 2) were quicker at handling live prey items; 3) were less reliant on supplementary feed which could be withdrawn; 4) developed different gut morphology. Consequently birds reduced the risk of predation by reducing exposure time whilst foraging, while allowing more time to be vigilant, were better at handling and discriminating natural food items and not solely reliant on supplementary feed and had a better gut system to cope with the natural forage. Post release survival was also improved when pheasants were reared with access to perches. We identified three mechanisms to explain this. Pheasants reared with access to perches had: 1) a physiology to better enable the birds to fly to the higher branches and cope with prolonged roosting; 2) a higher propensity to roost off the ground at night; and 3) more accurate spatial memory. Consequently, birds were at a reduced risk of terrestrial predation by roosting at night, and accurately remember their new environment upon release. I also showed that these manipulations did not compromise the welfare of the individuals prior to release, as often feared when trying to create a naturalistic environment to a captive population.

An additional mechanism that can affect the success of a translocation programmes, operating at the level of the population, considers the optimality of the mixture of released individuals that can influence a release programme. The personality of birds within a released population, tested prior to release into the wild, influenced their fate and dispersal. I suggest a number of release mechanisms that would aid the survival of a diverse range of behavioural types that are essential for the production of a self-sustaining population in a fluctuating environment.

I showed that harem size is strongly influenced by the vigilance behaviour of its constituent members. Despite a shared interest in increasing harem size, their optimal size is influenced by trade-offs in individual vigilance behaviour, resulting in relatively small harems, perhaps leading to females associating with less preferred males, and males being surrounded by fewer females than they could mate with. The aim of this study was to provide the background to future work trying to promote developments to allow for better reproductive success.

I finally discussed these results and how they add to the current knowledge of captive-rearing and release, and examine the wider implications of my results from the pheasant rearing system for reintroduction biology. I calculate the likely costs of interventions and extrapolated the potential economic and environmental benefits of implementing changes to the current methods of rearing.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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My philosophy during the PhD was that “to study the behaviour of a pheasant one must become the pheasant”. This involved waking up at the crack of dawn and going to bed after the birds had gone to roost. This lifestyle was made easier by Pamela Barlow who was happy for me working these hours as long as I found time to visit NYC. On Pam’s visits to Hampshire, although I planned for time off during these periods, we still managed to spend 2 days building (and rebuilding) pheasants pens, 2 cold December days collecting birds, 2 days of *post mortem* analyses and the odd day conducting behavioural observations. When we were not in the same country Pam would speak to me every day on SKYPE, read through work, listen to presentations and assist with data entry, but most importantly Pam gave me the enthusiasm to go out for that extra session and collect that vital data point. Without Pam’s patience, enthusiasm, witticisms and love the PhD may have been too much.

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DECLARATION

This thesis contains five data chapters, each of which is written as a manuscript for publication, and is therefore intended to stand alone. With this, some information may be redundant or repeated. While the candidate made substantial contributions to the manuscripts and is fully responsible for the work presented in this thesis, where the first person is used in the manuscripts it is used in the plural ('we') to reflect contributions from co-authors and /or field assistants. Contributions by co-authors are detailed for each manuscript below. Dr Joah Madden was involved in designing the project, guided data collection and provided comments on drafts of all chapters.
All data used in this thesis was collected during the period of the PhD.

Chapter 2: **Diet complexity in early life affects survival in released pheasants by altering foraging efficiency, food choice, handling skills, and gut morphology**
Whiteside MA., Sage R., Madden JR.
The candidate designed the rearing facility and subsequent fieldwork with guidance from Dr Joah Madden and Dr Rufus Sage, collected the vast majority of the data collection, analysed the data and wrote the manuscript. All authors and two anonymous referees provided feedback on drafts. The paper was submitted to *Journal of Animal Ecology* in November 2014, and resubmitted following major revision in March 2015, accepted April 2015.

Chapter 3: **Structural complexity in early life affects survival in released pheasants by altering roosting propensity, physiology and spatial cognitive ability**
Whiteside MA., Sage R., Madden JR.
The candidate designed the rearing facility and subsequent fieldwork with guidance from Dr Joah Madden and Dr Rufus Sage, collected the vast majority of the data

collection, analysed the data and wrote the manuscript. All authors as well as Dr Tom Smulders and Sophie Turle provided feedback on drafts.

Chapter 4: **A successful reintroduction programme: the importance of pre-release welfare**

Whiteside MA., Sage R., Madden JR.

With guidance from Dr Joah Madden and Dr Rufus Sage, the candidate collected the vast majority of the data collection, analysed the data and wrote the manuscript. Dr Joah Madden provided feedback on drafts.

Chapter 5: **Dispersal and mortality: how personality can influence the success of restocking programs**

Whiteside MA., Sage R., Stratton T., Madden JR.

The candidate designed the testing arena with guidance from Dr Joah Madden and Timothy Stratton, substantially contributed to the data collection, analysed the data and wrote the manuscript. All authors provided feedback on drafts.

Chapter 6: **What limits harem size? Individual and group vigilance levels constrict opportunities for sexual skew**

Whiteside MA., Madden JR.

The candidate designed the fieldwork with guidance from Dr Joah Madden, substantially contributed to the data collection, analysed the data and wrote the manuscript. Dr Joah Madden provided feedback on drafts. The paper was submitted to *Animal Behaviour*; it was rejected and had feedback from reviewers.

Chapter One

Why do translocation programmes fail and how can they be improved?

1.1. Introduction

Pheasants (*Phasianus colchicus*) and red-legged partridges (*Alectoris rufa*) are reared in captivity and subjected to a series of annual restocking programmes in the UK. After release into the wild these birds suffer from poor survival and poor reproductive success (Anderson 1964; Brittas *et al.* 1992; Buner, Browne & Aebischer 2011). To overcome high post release mortality and poor reproductive success, every year the game industry releases high numbers of birds (*circa* 40 million) to maintain a harvest of around 35% that number (PACEC 2008). This poses a number of ethical, environmental and financial problems that needs to be addressed. The primary aim of this study is to discover methods of rearing pheasants that will aid future survival and reproductive success.

More generally, poor survival and poor reproductive success is not uncommon for animals that are reared in captivity and then released into the wild for conservation purposes, and is a major factor in why many translocation programmes fail (Kleiman 1989; Fischer & Lindenmayer 2000). The pheasant rearing and release system is analogous to those adopted for many conservation programmes. Unlike many conservation programmes the pheasant system allows for high sample sizes, multiple replicates and focussed post release monitoring that is often lacking in these programmes (Seddon, Armstrong & Maloney 2007; Armstrong & Seddon 2008). Therefore a secondary aim of the study is to use pheasants as a surrogate for reintroduction biologists.

Although large numbers of pheasants and red-legged partridges are reared and released each year, few empirical studies have been conducted on assessing the problems of the current rearing regimes and even fewer studies look to manipulate environments to help improve post release survival and reproductive success. Therefore, in this literature review I will draw on examples from across the spectrum of conservation and reintroduction biology to help identify why translocation programmes fail and then determine rearing environments that best promotes the development of behavioural, physiological and cognitive characteristics to maximise survival of the pheasant. I will utilise research from a range of taxa and from systems that use translocations for conservation and sporting purposes.

Halting the decline of endangered species through the use of captive release programmes has a long history. Despite the process being used on a wide diversity of species and recommended for many conservation efforts, the successes of these programmes are extremely poor (**Section 1.2**). Compared to wild animals and animals

translocated from a wild population source, captive reared individuals exhibit high mortality and poor reproductive success (**Section 1.4**). This poor success is attributed to behavioural, physiological and cognitive differences between captive and wild reared individuals (**Section 1.4.1**) as well as possible individual differences attributed to release populations (**Section 1.4.1.4**). Animals exhibit developmental plasticity and can acquire important survival characteristics through experience; however if important stimuli are absent or if adverse conditions are experienced during development, it is easy to see how developmental deficiencies can manifest. By understanding how captive environments differ from the wild it is possible to determine how manipulations to the environment can better prepare an animal for release (**Section 1.5**). By review this literature it is possible to determine why we see little evidence of enhancing the captive environment to promote survival skills for release programmes (**Section 1.6**).

The pheasant and partridge rearing system provide the solution to issues that plague reintroduction biology (**Section 1.7**). Current rearing and release methods (**Section 1.7.1**) result in poor post release survival, dispersal and reproductive success (**Section 1.7.2**), but manipulations to the rearing environment do show that these birds exhibit developmental plasticity (**Section 1.7.3**). Successful manipulations of a rearing environment in an effort to improve the success of the programme would bring economic, environmental and ethical benefit to the game-rearing industry (**Section 1.7.4**) but such benefits are not restricted to the industry itself (**Section 1.7.6**).

I conclude by summarising the review, and report how I intend to utilise this information to design an environment suitable for use by practitioners of captive breeding for release into the wild that is more naturalistic, will promote the development of important survival skills, improve individual welfare and provide potential environmental and economic benefits to rearers (**Section 1.7.8**).

1.2. Translocation programmes:

Halting the decline of endangered species by the protection of *in situ* populations is not always the best method to encourage a population's natural recovery; in some cases, the need for *ex situ* techniques becomes a necessity (Kleiman 1989). These techniques may require the displacement and movement of animals in an attempt to establish, re-establish, or augment a wild population (IUCN 1998).

The terminology relating to the movement of animals for the purpose of conservation is often inconsistent and has caused substantial confusion in the

literature. For the purpose of this literature review and future chapters I use the definitions as dictated by the original IUCN position statement in 1987 (IUCN 1987) whereby “the movement of living organisms from one area with free release into another” is referred to as a translocation. These translocations can be subdivided into three main categories: 1) introduction: moving of an organism to an area outside its historically native range; 2) reintroduction: moving an organism into a part of its native range from which it has disappeared or become extirpated in historic times; and 3) restocking: the movement of organisms with the intention of building up the numbers of individuals of that species in an original habitat (IUCN 1987). A later addition to the reintroduction guidelines restricted the term to only the movement of wild individuals (IUCN 1998), meaning that there was overlapping of definitions and no general term for the movement of animals. However, for clarity, I agree with Armstrong and Seddon (2008) thereby using ‘translocation’ as a ‘catch-all’ term and subsequent divisions being mutually exclusive to one another.

Translocation programmes can vary due to the behavioural and management concerns specific to the system and one major difference is the source population. Wild-caught individuals can be translocated from a sustainable wild population (IUCN 1998); this source is common in many successful translocation programmes, frequently focussed on game species including wild turkey (*Melegaris gallopavo*), bighorn sheep (*Ovis canadensis*), elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*) (Griffith *et al.* 1989; Wolf *et al.* 1996). However, sometimes captive propagation and then release into the wild, hereafter ‘release programme’, is the only tool available for conservation and becomes a necessity when: 1) there is an imminent chance of extinction (e.g. Mauritius kestrel (*Falco punctatus*) (Cade & Jones 1993); 2) the current habitat is unsuitable for a species, for instance due to habitat destruction or environmental contamination; (e.g. the introduction of the tree snake (*Boiga irregularis*) caused a rapid decline in Guam rail (*Gallivarus owstoni*) numbers; under threat of extinction remaining birds were brought into captivity and have successfully bred and been released back onto the island when the environment was habitable (Marshall 1985; Haig, Ballou & Derrickson 1990)); 3) the genetic diversity requires careful and meticulous intervention; often associated with small population sizes (e.g. in black footed ferrets (*Mustela nigripes*) (Miller *et al.* 1992; Biggins *et al.* 1998)); 4) restocking is required and there is no suitable wild source to obtain the supplementary animals without jeopardising the source population (e.g. Mississippi sandhill cranes (*Grus canadensis pulla*) (Ellis *et al.* 2000)): 5) a captive population is required to act as temporary safe guard, providing a haven while habitats are restored (e.g. Spekes

gazelle (*Gazella spekei*) (Templeton & Read 1984)); and 6) required to act as a source for education.

1.3. Failure of translocation programmes; Rise of reintroduction biology

There have been many attempts to define the criteria that have to be satisfied to determine a translocation programme as a success (Seddon 1999; Kleiman *et al.* 2000), including: 1) breeding by the first wild born; 2) a three year breeding population with recruitment exceeding adult death rate; 3) an unsupported wild population of at least 500; 4) the establishment of a self-sustaining wild population (Jule, Leaver & Lea 2008). There have been a number of review papers published indicating the success of translocation programmes based on these criteria or similar. Success rates for these programmes were very poor during the 1970s and 1980s (Griffith *et al.* 1989), and subsequent reviews show that this has not improved, with only 11% of all reintroduction programmes having any form of measureable success (Beck *et al.* 1994; Wolf *et al.* 1996; Fischer & Lindenmayer 2000). Even though translocation programmes have such poor success, and are often seen as a last resort in the establishment or reinforcement of a wild population (Hutchins, Willis & Wiese 1995), they were still recommended in 64% of recovery plans for endangered species in the US (Tear *et al.* 1993).

Different source populations may determine fitness consequences and ultimately the success of a project. The success rates for a translocation programme with a wild source population has been higher than for translocations which originated from a captive population (Wolf *et al.* 1996; Fischer & Lindenmayer 2000; Mathews *et al.* 2005; Jule, Leaver & Lea 2008). Less than 15% of studies using a captive bred population are successful in creating an established population (Griffith *et al.* 1989), whereas using animals from a wild source has a success rate of around 31 % (Fischer & Lindenmayer 2000). Although there has been much documented evidence for the failure of translocation programmes, there are examples of it working successfully, including the big horn sheep where captive bred individuals survival was equal to wild born sheep (Ostermann, Deforge & Edge 2001) and the Mauritius kestrel (*Falco punctatus*) showing no difference in survival between captive reared and wild individuals (Nicoll, Jones & Norris 2004).

As a result of this documented poor success, action was required and this led to the formation of the International Union for Conservation of Nature and Natural Resources Species Survival Commission (IUCN/SSC) Reintroduction Specialist Group (RSG). Its aim was to assist reintroduction practitioners in conducting viable

reintroduction projects worldwide by actively developing and promoting sound inter-disciplinary scientific information, policy, and practice to establish viable wild populations in their natural habitats (IUCN 1998).

Since this intervention, the number of translocation programmes reported increased exponentially in peer-reviewed publications during the 1990s. However, inadequate science plagued the research, particularly because the majority of translocation programs were being used as a management tool and not designed to meet research objectives, often releasing animals with little planning and unfocused monitoring, with retrospective analyses being conducted on descriptive accounts of the programme and as a result fundamental elements of the project were likely missed (Seddon, Armstrong & Maloney 2007; Armstrong & Seddon 2008).

A more scientific approach was required, with a more strategic approach to research and monitoring, where questions are identified *a priori* and designed to monitor specific levels focussed on the translocated animals' survival, their group compositions and dynamics, habitat use and any intrinsic factors that affect the response to the programme, as well as effect at the meta-population and ecosystem levels (Armstrong & Seddon 2008). The need for improvement in the practice of translocation and the science behind the work was recognised and the term "reintroduction biology" was coined (Armstrong & Seddon 2008).

Utilising this focussed monitoring it is possible to determine why we observe poor success in animals that are translocated, specifically why we observe better success in animals from a wild source population.

1.4. Problems with translocation programmes from captive sources

Captive reared animals released into the wild suffer from extremely high mortality (Kleiman 1989; Snyder *et al.* 1996); significantly higher than their wild conspecifics (Fischer & Lindenmayer 2000). More specifically see table 1.1.

Table 1.1. Percentage of founding population surviving depending on wild and captive sources

Species	Percentage of founder population surviving [captive (wild)]	Reference
Otter (*Lutra lutra*)	42 (79)	(Sjöåsen 1996)
Weasels (*Mustela nivalis nivalis*)	93 (98)	(Hellstedt & Kallio 2005)
Vancouver marmots (*Marmota vancouverensis*)	61 (85)	(Aaltonen *et al.* 2009)
Mexican wolf (*Canus lupus baileyi*)	35 (18)	(Oakleaf *et al.* 2004)
Grey Partridge (*Perdix perdix*)	30 (44)	(Parish & Sotherton 2007)
Pacific Salmon (*Oncorhyncus spp*)	10 (3)	(McNeil 1991)

Greatest mortality is often observed in the periods just after release (Musil, Connelly & Reese 1993; Olla, Davis & Ryer 1998), as this is a period when naïve individuals are forced into a novel and variable environment and exposed to predator risk and unpredictable forage (Brown & Laland 2001). This may be compounded by the observation that released animals show higher dispersal distances than would normally be expected in the wild (Stamps & Swaisgood 2007). This not only increases the risk of entering novel environments and encountering predators (Linklater & Swaisgood 2008), but it also diverts time and energy away from other important survival skills such as procuring shelter (Shier 2006).

In addition to reduced survival, captive reared individuals also often exhibit poor reproductive success when released into the wild. Wild reared piper plover (*Charadius melodus*) survived better, hatched 36% more eggs and fledged 56% more chicks than captive reared conspecifics (Roche, Cuthbert & Arnold 2008). Captive reared and released snowy plover (*Charadrius alexandrinus*) nested in lower quality areas compared to their wild companions (Page, Quinn & Warriner 1989). Survival and recruitment were higher in wild reared Aplomado falcons (*Falco femoralis septentrionalis*) compared to released birds (Brown *et al.* 2006). Hatchery reared and released Chinook salmon (*Oncorhynchus tshawytscha*) had smaller eggs and reduced reproductive success relative to wild populations (Heath *et al.* 2003). Ultimately, high mortality, poor reproductive success and high dispersal rates reduce the size of the

founding population and also reduce the likelihood of creating a self-sustaining population (Mihoub *et al.* 2011; Armstrong *et al.* 2013).

It is important to note that even though translocated animals from a wild source population can have greater success than those released from captive sources there are still issues with this form of translocation. Translocated individuals from wild sources often have lower fitness than local conspecifics, perhaps due to knowledge of local conditions (Sarrazin & Barbault 1996; Reed 1999), or because of the stress associated with the translocation (Teixeira *et al.* 2007; Dickens, Delehanty & Michael Romero 2010). Even short periods of time in captivity can cause increased stress levels for wild animals exposed to captivity (Coddington & Cree 1995; Gregory *et al.* 1996). For example stress during transport influenced survival of released rabbits (*Oryctolagus cuniculus*) (Letty *et al.* 2000).

It is clear that in most captive release programmes the released individual is unable to cope with the transition from captivity to the wild (Brown & Laland 2001). One cause may be due to the genetic differences between wild and captive reared individuals, which can arise if a small founder population in captivity are highly inbred or genetically adapted to conditions different to those found at the site of release (Armstrong & Seddon 2008). However, although released animals traditionally have low survival and reproductive success, their surviving wild offspring may be equally successful as their wild peers (Sage *et al.* 2003), suggesting that physical and behavioural characteristics influenced by early life experiences are at fault in captive-reared individuals rather than underlying genetic deficiencies (Snyder *et al.* 1996; van Heezik & Seddon 1998).

1.4.1. Mechanisms behind poor success

An important focus for reintroduction biologists has been to determine what characteristics are deficient in released animals compared to wild conspecifics, and how these may cause individuals to exhibit high mortality, dispersal and poor reproductive success. Such ‘developmental deficiencies’ can be divided into three main areas which focus on the individual: behavioural, physiological and cognitive. An additional mechanism operating at the level of the population considers the optimality of the mixture of released individuals.

1.4.1.1. Behavioural deficiencies

Animals from a captive source often show a lack of wild type behaviours (Snyder *et al.* 1996; Rabin 2003). Therefore the simple method to determine what characteristics are at fault for the failure of a translocation programme is to compare the behaviour of the released animal with those of the more successful wild conspecific.

Predation is a major cause of mortality of released individuals, specifically to predator-naïve animals (Griffin, Blumstein & Evans 2000). Poor predator detection and avoidance behaviours of released individuals is believed to be a reason for this (Griffin 2004). Captive born rhesus monkeys (*Macaca mulatta*) show no fear of snake-like objects, whereas the same stimuli elicited avoidance and fear responses in wild conspecifics (Cook & Mineka 1989). Hatchery reared fish generally failed to avoid predators and suffered from high mortality (Olla, Davis & Ryer 1998). Mortality is not simply restricted to predator recognition: captive reared and released Oldfield mice (*Peromyscus polionotus subgriseus*) were slower to enter a burrow and used refuges less often than their wild counterparts (McPhee 2003). Captive born weasels (*Mustela nivalis nivalis*) were more visible in the field and less timid than wild caught weasels (Hellstedt & Kallio 2005).

Many individuals suffer from starvation after release into the wild, which has been attributed to incorrect food acquisition (Ellis *et al.* 2000). Cod (*Gadus morhua*) reared on pelleted food were less efficient at capturing live gobies than wild cod (Steingrund & Fernö 1997). In some cases released turbot (*Scopthalmus maximus*) have been observed consuming stones and pebbles as it closely resembles the pelleted food consumed in the hatchery (Ellis, Hughes & Howell 2002). Bank voles (*Clethrionomys glareolus*) in captivity were unable to open nuts that were easily opened by wild conspecifics (Mathews *et al.* 2005).

Aberrant social behaviour is often exhibited by captive animals released into the wild (Kleiman 1989; Fleming & Gross 1993). In birds, wild reared takahe (*Porphyrio mantelli*) remained sedentary with their territorial parents at a year old, whereas captive reared birds wandered alone more widely (Maxwell & Jamieson 1997). Similar patterns are seen in fish. Released coho salmon (*Onchorhynchus kisutch*) were competitively inferior to wild fish (Fleming & Gross 1993). Wild Atlantic salmon (*Salmo salar*) were more dominant and more likely to win a competitive bout than captive reared salmon (Metcalfe, Valdimarsson & Morgan 2003).

The ability to move around a novel, variable and complex environment is an important skill for released animals. However movement patterns and dispersal often differ in released animals. Released captive bred dormice (*Muscardinus avellanarius*) travelled significantly less far from the nest each night compared to wild dormice, suggesting they would reduce their chances of locating natural food sources and that they were slower to establish in the novel environment (Bright & Morris 1994). Released kaki (*Himantopus novaezelandiae*) often dispersed from their release site and also therefore left a managed area specifically designed and managed to help them survive (van Heezik, Maloney & Seddon 2009). Conversely, in some cases newly released individuals move too little. This is particularly important in high-number release programmes because high densities increase the risk of disease (Steinhaus 1958) and an accumulation of waste that can attract predators (Banks, Norrdahl & Korpimäki 2002).

1.4.1.2. Physiological deficiencies

A characteristic that is more difficult to quantify in released animals, but is equally important, is the physiological development associated with captive rearing. Captive reared Attwaters prairie-chickens (*Tympanuchus cupido atwateri*) had poorer flying ability in terms of shorter flight distances and endurance; functions attributed to poor muscle development due to the captive rearing environments (Hess *et al.* 2005). Wild reared northern bobwhite quail (*Coliinus virginianus*) had greater flight speed and greater flight distance than captive reared quails (Perez, Wilson & Gruen 2002).

Susceptibility to parasites and disease after release is a major factor in post-release mortality (Viggers, Lindenmayer & Spratt 1993; Cunningham 1996; Woodroffe 1999), and often captive reared animals are more susceptible to disease than wild conspecifics (Jule, Leaver & Lea 2008).

1.4.1.3. Cognitive deficiencies

Recent evidence suggests that artificially reared fish have smaller brains and lower cognitive abilities compared to their wild counterparts (Marchetti & Nevitt 2003; Kihslinger & Nevitt 2006). Even first generation laboratory reared guppies had smaller telencephalon and optic tectum than wild caught guppies (Burns, Saravanan & Helen Rodd 2009). A lack of access to wild stimuli may restrict the development of important cognitive process, for instance having access to a variety of food types may help develop cognitive aspects of foraging behaviour (Thornton & McAuliffe 2006). These cognitive deficiencies could reduce an individual's ability to utilise novel resources and acclimatise to a novel environment (Reader & Laland 2003; Sol *et al.* 2008).

1.4.1.4. Suboptimal mixture of released individuals

This review so far has concentrated on how manipulations of rearing conditions influence the development of important survival characteristics for the individual. However, individuals are usually released as part of a social grouping, however loose, and thus their success is likely highly dependent on the others in their released cohort. Individuals typically exhibit distinct personality types which capture consistent behavioural responses across contexts, with five major dimensions or continuum studied; boldness, exploration, activity, sociability and aggressiveness (Réale *et al.* 2007). Most studies are conducted on animals in captivity, however applying personality to conservation has been adopted (McDougall *et al.* 2006) and a better integration of the underlying theory with practical application is recommended (Watters & Meehan 2007). Personality predicts ecologically relevant behaviours such as dispersal and mortality (Réale *et al.* 2007); both of which reduce the size of the founder population and the likelihood of creating a self-sustaining population (Armstrong & Seddon 2008; Mihoub *et al.* 2011; Armstrong *et al.* 2013). Released animals show higher dispersal distances than would normally be expected in the wild (Stamps & Swaisgood 2007). This not only increases the risk of entering novel environments and predators (Linklater & Swaisgood 2008), but it also diverts time and energy away from other important survival skills such as procuring shelter (Shier 2006). Dispersal is often linked with personality, for instance, released killifish (*Rivulus hartii*) that were personality tested in the laboratory and released into native streams showed increased dispersal if they were bold (Fraser *et al.* 2001). Bold swift foxes (*Vulpus velox*) moved around the release site more than shyer foxes (Bremner-Harrison, Prodohl & Elwood 2004). Typically bold individuals have higher rates of mortality (Réale *et al.* 2007), as a function of their increased risk taking behaviour (Smith & Blumstein 2008).Therefore, personality can also have direct influences on fitness components (Réale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Dingemanse & Réale 2005; Cote, Dreiss & Clobert 2008; Smith & Blumstein 2008). All these factors can impact the success of a translocation program (McDougall *et al.* 2006).

Many studies concentrate on boldness or activity and its effect on post-release behaviour. A continuum that receives less attention is social tolerance. There is evidence of social tolerance in captive populations of Japanese quail (*Coturnix japonica*), identifying differences in motivation to join a group as juveniles persisting into adulthood (Jones *et al.* 2002). Social tolerance may be density dependent; less socially tolerant common lizards (*Lacerta vivpara*) dispersing further than more tolerant individuals (Cote & Clobert 2007). Many release programmes are highly focussed and

use relatively low numbers, the effects of personality within high release numbers have received little attention.

It is important to understand how personalities within the release population are affected by environmental pressures and from this determine the best release strategy. With this there is a potential to amend release protocols. This could either be by selecting personality traits that best fit the population as suggested by Watters, Lema and Nevitt (2003), or by creating an environment that allows for the reintroduction and establishment of many personality types, as suggested by (Bremner-Harrison, Prodohl & Elwood 2004). The second may seem crucial in terms of reintroduction biology because an important aspect of the release is to maximise genetic diversity among the release animals. Genetic and behavioural diversity reduces the chances for founder effects and inbreeding depression, which can compromise small populations struggling to establish in a fluctuating environment (Kleiman 1989; Watters, Lema & Nevitt 2003; Watters & Meehan 2007; Reading, Miller & Shepherdson 2013).

1.5. Captive rearing; how conditions differ from the wild and measures used to improve it

Differences between the wild and captive environments seem to cause the differences in developmental trajectories, but, typical captive environments for animals prior to release are often defined by their convenience for the rearing organisation, rather than for developmental or welfare considerations (Olsson & Westlund 2007). I highlight three areas in which captive conditions differ from the natural environment: 1) absence of parents; 2) non-naturalistic, therefore a lack of environmental complexity, lack of predators and a lack of naturalistic diet; and 3) welfare.

1.5.1. Absence of parents

In some cases captive managers are required to rear animals with an absence of parents or informed young peers because of logistical issues, for instance the mother may not adapt to captive conditions therefore the manager is required to intervene before the offspring suffer from malnutrition or cannibalism. Some conservation protocols facilitate restoration by removing multiple clutches from wild pairs allowing caretakers to artificially rear the initial broods in captivity and wild adults to rear subsequent broods (Powell & Cuthbert 1993; Wood & Collopy 1993). The life history of the species can influence management decisions, where the survival of the young is not always beneficial under parent rearing, particularly important in birds with asynchronous hatching and high risk of siblicide (Kreger *et al.* 2004).

Mother-offspring bonds are established at parturition and hatching and are important for development of some critical behaviours (Nowak 1996). Firstly, offspring often require nutritional sustenance from their parents, but also mother-offspring relationships create emotional interactions that can impact post-independent activity, communications, behavioural acquisition and learning (Moberg & Wood 1982; Cheyne, Chivers & Sugardjito 2007). This is important when learning important survival skills such as food discrimination and foraging techniques (Thorhallsdottir, Provenza & Balph 1990; Thornton & McAuliffe 2006; Thornton 2008) as well as predator detection and avoidance (Griffin, Blumstein & Evans 2000; Griffin 2004). Many precocial chicks actively follow their mother with the help of contact calls (Collias & Joos 1953). Juvenile French grunts (*Haemulon flavolineatum*) learn migration routes between schooling and foraging sites from following adults, fish that were precluded from following learned conspecifics did not follow the same migration route or use the same foraging sites (Helfman & Schultz 1984). Guppies (*Poecilia reticulate*) that watch learned conspecifics will adopt the same path they used, even if it is more costly than alternative routes (Laland & Williams 1997). Foraging ants (*Formica rufa*) use pheromone signals to help individuals through a complex environment (Denny, Wright & Grief 2001).

Rearing without access to parents or learned conspecifics has a marked effect on post release behaviour and survival. Hand reared houbara bustards (*Chlamydotis undulata*) exhibited poorer anti-predation behaviours compared to birds reared with parents (van Heezik, Seddon & Maloney 1999). Parent reared whooping cranes (*Grus americana*) were more vigilant and had better foraging ability compared to birds reared without parents (Kreger *et al.* 2005). Hawaiian geese (*Branta sandvicensis*) reared without access to parents or foster parents were less vigilant after release and less likely to join a social group compared to parent reared birds (Marshall & Black 1992). Black-tailed prairie dogs reared without access to adults reduced wariness to predators after release resulting in poorer survival compared to parent reared conspecifics (Shier & Owings 2007).

In captive systems that are required to rear without parents or learned conspecifics, efforts have been made to provide stimuli that simulate social learning, without the need for the learned conspecific to be present. This has had some success. TV screens showing a pre-recorded video of adult rhesus monkeys exhibiting a fear response to a snake caused the naive observer to perform a similar fear response to the same conditioned stimuli (Mineka & Cook 1988). An abstract method of simulating social learning has been adopted in chickens, where a motorised arrow was used to replicate pecking movements to act as a social stimulus for one-day old chicks; chicks

showed a preference for arrow-pecked stimuli (Bartashunas & Suboski 1984; Suboski & Bartashunas 1984).

Few studies have looked at manipulating rearing conditions prior to release to influence survival of a release programme by the provision of a “learned conspecific” to promote social learning. One abstract method is the use of “puppets”, where under human control puppets can be used to stimulate filial imprinting and induce social learning. Puppet reared Mississippi sandhill cranes improved foraging behaviour resulting in survival equal to parent reared birds (Ellis *et al.* 2000). Puppet reared ravens (*Corvus corax*) were more careful of caretakers and more vigilant prior to release and had better survival after release into the wild compared to hand reared birds (Valutis & Marzluff 1999). Puppet reared takahe (*Porphyrio mantelli*) had equal likelihood of survival as wild reared individuals (Maxwell & Jamieson 1997).

1.5.2. Non-naturalistic environment

The natural environment is often full of sensory stimuli, in contrast artificial rearing facilities are much less variable and therefore animals in these systems may be deprived of sufficient input for proper development (Blaxter 1970). A common method used to alleviate issues associated with captivity is the use of environmental enrichment. Early environmental enrichment programmes in captive populations looked at broad goals, specifically targeting welfare parameters (Shepherdson, Mellen & Hutchins 1998), such as the reduction in abnormal behaviours (Carlstead, Seidensticker & Baldwin 1991; Markowitz, Aday & Gavazzi 1995; Grindrod & Cleaver 2001) and increasing space utilisation (Williams *et al.* 1996). In more recent years, following the establishment of reintroduction biology, we have seen more captive populations being subjected to treatments with the aim of understanding the mechanisms behind the development of survival skills that could be beneficial for released animals (Reading, Miller & Shepherdson 2013). This shift in emphasis meant that environmental enrichment was only deemed successful when certain characteristics were acquired, with the ultimate aim of being no longer able to discern any developmental differences between wild and captive bred animals (O'Regan & Kitchener 2005).

1.5.2.1. Lack of complex environment

In the wild an individual is required to orientate and navigate in a complex environment, especially to locate food, mates or home. There are a number of processes that animals use to facilitate navigation, including path integration, the use of

landmarks, and the use of geometric relationships (review see Pearce 2007). Navigation can also be assisted by social learning (see section 1.5.1.).

Captive rearing typically takes place in unnatural and often spatially simple habitats (Brown & Laland 2001; Braithwaite & Salvanes 2005). Manipulating the captive rearing environment by creating a more complex and naturalistic habitat may provide enhanced opportunities for learning which in turn affects neural development, cognitive performance and adult behaviour. Brain or brain region size is dependent on the spatial complexity of the habitat experienced during rearing (Kihslinger & Nevitt 2006; Burns, Saravanan & Helen Rodd 2009; Näslund *et al.* 2012). For instance, zebra fish (*Danio rerio*) reared in enriched environments increased their brain cell proliferation, in particular in the telencephalon (von Krogh *et al.* 2010). Atlantic salmon reared in an environment containing temporary and variable structural environmental enrichment had greater neurogenesis, particularly in the telencephalon, which manifested in to greater learning ability in the form of escaping a maze and speed at finding shelter (Näslund *et al.* 2013; Salvanes *et al.* 2013). Marsh tits (*Parus palutris*) that were allowed to store and retrieve food showed a cumulative increase in volume of the hippocampal region (Clayton & Krebs 1994). Domestic chickens (*Gallus gallus domesticus*) exposed to a spatially complex rearing environment during ontogeny were better at spatial cognitive tasks, such as navigating the environment (Gunnarsson *et al.* 2000; Wichman *et al.* 2007).

Anti-predator behaviour can be influenced by creating a more naturalistic captive environment. Cod, Atlantic salmon and seabream (*Diplodus* sargus) adopted less risky behaviour as adults when released into a novel environment if reared with access to shelters compared with conspecific reared in barren environments (Salvanes & Braithwaite 2005; Roberts, Taylor & Garcia de Leaniz 2011; D'Anna *et al.* 2012) . Manipulations to tank substrates to replicate more natural sand may provide opportunities to learn burying behaviour in benthic species like sole (*Solea solea*) (Ellis, Hoowell & Hughes 1997). Domestic chickens reared with access to perches were more likely to perch as adults (Newberry, Estevez & Keeling 2001).

A more complex environment can initiate morphological changes that mean the individual can move more effectively through such complex habitats (Ganduno-Paz, Couderc & Adams 2010). Steel head (*Oncorhynchus mukiss*) reared in enriched conditions, in the form of submerged structures, overhead cover, and underwater feeders, had greater dorsal fin quality than those reared in conventional tanks, and their fin sizes were similar to those observed in wild conspecifics (Berejikian 2005).

Zebrafish reared in a structurally complex environment grew slower and were smaller than fish reared in a barren environment, which may have been stimulated by amplified competition for food in a more structurally complex environment (Spence, Magurran & Smith 2011). The addition of perches in intensively reared chicken environments allowed for a degree of physiological development not possible in chickens reared in barren environments; mechanical loading associated with mounting and dismounting perches combined with static loading associated with balance caused greater bone mineralisation (Reichmann & Connor 1977; Hughes & Appleby 1989), bone mass (Shipov *et al.* 2010), bone volume (Hughes *et al.* 1993), and bone strength (Fleming *et al.* 1994). A barren and confined captive environment is to blame for poor flight development in the Atwatters prairie chicken as it restricts the development of flight muscles (Hess *et al.* 2005).

Very few studies have looked to manipulate habitat complexity to influence post release behaviour and survival. A study on golden lion tamarins (*Leontopithecus rosalia rosalia*) reared with a more complex environment had differences in locomotor and foraging behaviours compared to cage reared conspecifics reared with fixed food, inflexible substrate and fixed travel routes, there was no difference in post release survival (Stoinski & Beck 2004). Steelhead reared in a habitat enriched tank were more socially dominant after release than others reared in laboratory conditions (Berejikian *et al.* 2000).

1.5.2.2. Lack of predators

Managers of captive wild animals frequently want to create an environment that is free from fear (FAWC 1993). One way to achieve this is by excluding predators. However, predator avoidance behaviours are essential for a released individual and often require previous exposure. As a result captive born rhesus monkeys show no fear to snake-like objects, whereas their wild conspecifics when exposed to the same stimuli exhibited avoidance and fear responses (Cook & Mineka 1989). Predator avoidance learning through observational conditioning requires a predatory cue, considered the conditioned stimulus, and an alarmed demonstrator, the unconditioned stimulus. Learning occurs when the conditioned stimulus and the unconditional stimulus are presented together to create an unconditioned response (Mineka & Cook 1993). Various fish species can learn from the chemical stimuli given from the skin of injured conspecifics as well as visual cues (Brown 2003; Griffin 2004). Terrestrial animals use a combination of compound visual and acoustic alarm cues (e.g. mobbing behaviours) as well as alarm vocalisation (Griffin 2004). This form of socially acquired avoidance has been seen in fish (including the common minnow (*Phoxinus phoxinus*)

(Magurran & Higham 1988) fathead minnow (*Pimephales promelas*) (Mathis, Chivers & Smith 1996), zebra fish (Suboski *et al.* 1990) and chum salmon (*Oncorhynchus keta*) (Ryer & Olla 1991)), birds (including the herring gull (*Larus argentatus*), lesser black backed gull (*Larus fuscus*) (Kruuk 1976), blackbirds (*Turdus merula*), New Zealand robins (*Petroica australis*)(McLean, Hölzer & Studholme 1999)), and mammals (including wallabies (*Macropus eugenii*), and moose (*Alces alces*) (Berger, Swenson & Persson 2001)).

One method to improve anti-predation behaviour is to rear animals in the presence of predators. Mexican fish (*Skiffia multipunctata*) reared in a naturalistic environment with predators, were less likely to approach model predators compared to fish reared in barren environments (Kelley, Magurran & Macías-Garcia 2005). Adding predator fish to captive salmon environments caused these individuals to be more wary than fish reared without predators (Roberts, Taylor & Garcia de Leaniz 2011). Another method to promote anti-predator behaviour in captivity, without the need for the predator to be active, is through the use of conditioning techniques (Griffin, Blumstein & Evans 2000). For instance, New Zealand robins that were presented with a model predator paired with a species specific alarm call resulted in a fear for that predator (McLean, Hölzer & Studholme 1999). Live predators can be used to simulate attacks (McLean *et al.* 2000). Humans can replicate aversive stimuli by using chases or capture simulation (Mesquita & Young 2007). Combining a predator and a simulated catch-up in captive born rhea (*Rhea Americana*) produced better antipredator behaviours compared to control birds (de Azevedo & Young 2006).

There has been some success arising from the addition of predators, or predatory stimuli to promote post release anti-predation behaviour and survival. Captive black tailed prairie dogs (*Cynimys ludovicianus*) conditioned to predators during early development were more vigilant and had better survival after release into the wild than untrained companions (Shier & Owings 2006). Captive-reared Chinook salmon (*Oncorhynchus tshawtyscha*) exposed to an 'injured fish' stimulus plus a predatory odour exhibited more adaptive foraging behaviour and spent more time in safer areas than control fish, resulting in better survival (Berejikian *et al.* 1999). White seabream reared alongside predators had greater flight distances and lower time to find a shelter when released into the wild compared to control fish (D'Anna *et al.* 2012). However, even though there is substantial evidence that conditioning can increase anti-predator behaviour in captivity, there is a surprising lack of empirical studies conducted on animals reared for release (van Heezik, Seddon & Maloney 1999; Griffin, Blumstein & Evans 2000). A reason for the lack of studies could be linked to conditioning methods

potentially training incorrect behavioural displays or habituating to predators (Starling 1991). In addition there are a number of ethical and behaviour issues associated with using conditioning techniques (see table 1.2).

Table 1.2. Advantages and disadvantages of conditioned and unconditioned stimuli for training animals to cope with predators (from Griffin, Blumstein & Evans 2000)

Stimulus	*Stimulus type*	*Advantages*	*Disadvantages*
Conditioned	Live predator	Richer stimulus Many reinforcers inherent to stimulus More appropriate for generalisation to occur	Risk of attack Ethical considerations Disease Logistics Less control over eliciting stimuli
	Model predator	No possibility of attack More control over eliciting stimuli Fewer ethical concerns Disease less likely No logistical problems	Stimulus activates fewer sensory modalities Fewer reinforcers inherent to stimulus
Unconditioned	Unpleasant stimulus (e.g. water squirts)	Technically straight forward	Does not mimic a predatory event
	Frightening stimulus (e.g. being chased, loud noises)	Closely associated with predatory event	Technically difficult if a standardised stimulus is required
	Natural signals (e.g. alarm calls)	Closely associated with predatory event Potential to exploit species specific learning mechanisms	Some options are technically difficult
	Painful stimulus (e.g. electric shock)	Highly salient	Unlikely to be associated with a survivable predatory even. Raises ethical concerns

1.5.2.3. Lack of naturalistic diet

Diet in captive environments is often non-natural, uniform, predictable, and presented repeatedly in the same locations (Huntingford 2004; Homberger *et al.* 2014). Many intensively reared ungulates and avian rearing systems constrain diet by using monotonous food rations (Villalba, Provenza & Manteca 2010; Ferretti *et al.* 2012). This diet may be nutritionally balanced and in excess but this means that the animals have

little need to search actively for food (Olla, Davis & Ryer 1998). In addition it may not give the animal the diverse dietary experiences that it would have if it was foraging in the wild.

Foraging behaviour works as a "nutritional complex" between food discrimination, food preference, handling ability and gut morphology (Thomas 1987), much of which requires previous experience in order to develop (Kitchener 1999).

1.5.2.3.1. Food discrimination learning

In the wild, food discrimination may be aided by local enhancement, when an individual will draw the attention of others to a particular location. This process is believed to be the reason young finches (*Fringillidae*) (Turner 1964) and canaries (*Serinus canaries*) (Cadieu, Cadieu & Lauga 1995) feed close to their parents in the wild. Adult white-tailed ptarmigan (*Lagopus leucurus*) produce unique vocalisations when specific high protein forage is encountered (Allen & Clarke 2005). If domestic chicken hens observed their chicks eating a food source that they experienced as being unpalatable they increased behavioural displays to direct their chicks towards more palatable food sources (Nicol & Pope 1996; Nicol 2004; Nicol 2006). Food discrimination may also be learnt socially by stimulus enhancement, where the behaviour of an individual draws the attention of a naïve individual to a particular item (Whiten & Ham 1992). Burmese jungle fowl (*Gallus gallus*) used the observations of others in their choice of feeding stations (McQuoid, Galef & 1992). Young domesticated chicken will eat otherwise avoided food colours following observation of a demonstrator (Johnston, Burne & Rose 1998). Stimulus enhancement is not restricted to vertebrates, for instance an observer bumble bee (*Bombus impatiens*) will go to the same colour flower as the demonstrator (Worden & Papaj 2005).

1.5.2.3.1. Food preference learning

Once attracted to a particular area the food preferences can be learned. This can be achieved through individual learning whereby ingesting a food type causes an autonomic response and a preference to that food type (Distel & Provenza 1991; Provenza 1996). Black footed ferrets given access to a diet of prairie dog early in life had a preference for this food item when adult (Vargas & Anderson 1996). There is also evidence for preferences to be socially learned and therefore consumption is not required. Observer rats can base their food preference on odour cues of demonstrator rats (Galef *et al.* 1988). Alarm calls and visual disgust based on others eating food laced with pepper is enough of a deterrent for tamarin monkeys (*Saguinus oedipus*) to

avoid that food source (Snowdon & Boe 2003). Domestic chicken as young as two days old are able to inhibit pecking at a potentially dangerous item by watching a demonstrator's behaviour alone (Nicol & Pope 1996; Salva *et al.* 2009).

1.5.2.3.1. Food handling learning

Handling food items often improves with experience and can influence survival and reproductive success (Rovero, Hughes & Chelazzi 1999; Thornton 2008). Meerkat (*Suricata suricatta*) pups are given otherwise inaccessible prey items from their parents or helpers, in the form of dead or disabled prey in order to learn handling techniques. The provision of these items causes pups to then rapidly and safely kill and consume dangerous prey items (Thornton & McAuliffe 2006). Pine-forest dwelling rats (*Rattus rattus*) diet consists almost entirely of pine seeds. Rats captured outside of the pine forest were unable to remove the tough outer scales of the pine cone and had a success in accessing seeds of less than 3%. However, 100% of rats reared with mothers in the pine forests successfully accessed the seed (Zohar & Terkel 1996).

Manipulation of early-life diet to better replicate natural conditions can improve foraging efficiency and enhance exploratory behaviour in captive salmon (Braithwaite & Salvanes 2005; Lee & Berejikian 2008). Captive black footed ferrets were more likely to make a successful kill as adults if they were provided with live hamsters (*Mesocricetus auratus*) during early development (Vargas & Anderson 1999). Having access to moving prey items improved post release foraging ability of black-footed ferrets resulting in an increase in survival compared to individuals reared with stationary food items (Biggins *et al.* 1998; Biggins *et al.* 1999). Atlantic salmon reared with variations in food distribution had a two-fold increase in survival compared to individuals reared with standard forage distribution system (Hyvärinen & Rodewald 2013). Captive reared Atlantic salmon reared in an unpredictable and enriched environment, with overhead shelter, varying water depth and direction and alterations in food dispersal expressed higher feeding rates than parr reared in barren environment with predictable diet provision (Rodewald, Hyvärinen & Hirvonen 2011). Food distribution may be able to influence the ability to compete in social interactions, for instance the clumping of food sources helps hone important competitive skills in captive hamadryas baboons (*Papio hamadryas*) (Gore 1993). Golden lion tamarin provided with puzzle feeders, which are highly defendable, caused individuals to use different strategies to obtain their ration, whether through direct competition, sharing or stealing (Rapaport 1998).

Altering early-life diet can affect physiology as well as behaviour. The gut is highly plastic and can change with diet. Most herbivorous animals are large and

terrestrial, enabling a capacity for a complex gastro-intestinal system (Robbins 1993). Red deer (*Cervus elaphus*) enlarge their alimentary canal when subjected to poor quality forages early in life (Milne *et al.* 1978). However, birds are precluded from simply enlarging gut size due to the energetic costs of flight increasing proportionally to mass (Dudley & Vermeij 1992). Therefore, birds typically develop more efficient guts rather than simply larger ones. One exception are red grouse (*Lagopus lagopus scotica*) that eat coarser, more fibrous, food in early life have bigger guts as adults than birds eating a finer and less fibrous diet (Moss 1972). This is important to grouse flight performance because grouse ceca, when full, represents 5% of total body mass (Moss 1983).

Even though theoretically the provision of a natural diet seems simple, the use of a more naturalistic diet is rarely tested on animals destined for release into the wild.

1.5.3. Welfare

Captive rearing can have a marked effect of welfare, with animals in captivity exhibiting more stress than their wild counterparts (e.g. cheetah (*Acinonyx jubatus*) (Terio, Marker & Munson 2004)). Poor welfare in captive populations is often related to stress (Morgan & Tromborg 2007) and can impact a release programme in three ways: 1) stress can influence physiological and neural development (McEwen 1999; Cam, Monnat & Hines 2003), particularly important development that may aid survival and reproductive success (Sedinger, Flint & Lindberg 1995; Nowicki *et al.* 2000; Alonso-Alvarez *et al.* 2006); 2) stress upon release can influence an ability to cope with disease (Homberger *et al.* 2013); and 3) stress is linked to the production of stereotypical behaviours (Mason *et al.* 2007), of which persistence into the wild can increase risk of predation (Vickery & Mason 2003). Stereotypical behaviours are seemingly purposeless repeated behaviours that are invariant in form (Mason 1991). These stereotypies are conspicuous in nature and can influence post release survival because once these behaviours have been learnt they are difficult to 'unlearn' (Mason *et al.* 2007). This persistence can make the released individual susceptible to predation (Vickery & Mason 2003). Although these behaviours are easily seen and can be extracted from the release population there are other smaller effects that are less discernible such as decreased behavioural flexibility and reduced attention to the environment all which can increase risk of predation but not as simple to identify and remove prior to release (Vickery & Mason 2003).

An absence of parents or early weaning can have welfare implications (Napolitano *et al.* 2002b). Lambs reared in isolation exhibit more stereotypical

behaviours such as flank touches (Moberg & Wood 1982). Early weaning often promotes the expression of non-normal behaviours such as appetitive or consummatory behaviours directed towards inappropriate objects and other peers (Le Neindre 1993; Napolitano *et al.* 2002a). A barren or non-naturalistic environment can compromise welfare, particularly if the environment does not have the features necessary for animals to perform their natural behavioural repertoire (Clubb & Mason 2003). The prevention of performing these natural behaviours can increase frustration and stress (Dawkins 1988; Mason, Cooper & Clarebrough 2001). Chickens exhibit increased coping mechanisms such as stereotypical pacing and preening displacement when they are denied access to naturalistic feed, nesting, incubation and sexual activity (Duncan & Wood-Gush 1972d; Blokhuis 1984; Olsson & Keeling 2000). Thwarting burrowing in captive pygmy rabbits (*Brachylagus idahoensis*) can lead to increased stress responses (Scarlata 2010). The provision of a less natural environment caused water voles to have lower leukocyte coping capacity than those reared in laboratory conditions (Moorhouse *et al.* 2007) suggesting that the non-natural conditions increased stress (McLaren *et al.* 2003). A less complex feeding regime caused rats to not be able to perform natural foraging behaviour and increased time conducting frustration behaviours (Johnson, Patterson-Kane & Niel 2004). A barren and non-naturalistic environment may not permit individuals to escape attacks by others. Captive chickens reared without natural perching or cover were subjected to more aggressive interactions compared to birds reared with more naturalistic environments (Olsson & Keeling 2000; Cordiner & Savory 2001; Donaldson, Ball & O'Connell 2012).

An important issue not generally considered is that these captive rearing conditions often house animals in higher numbers than would occur in the wild (Morgan & Tromborg 2007; Gelling *et al.* 2010). This overcrowding, or housing animals in abnormal social groupings, can induce chronic stress (Morgan 2007). Higher density is linked to increased aggression in intensive rearing systems such as pecking in domestic chicken (Nicol *et al.* 1999; Zimmerman *et al.* 2006). Lower leukocyte coping capacity in water voles (*Arvivola terrestris*) indicates immunosuppression and together with weight loss can be indicators of stress in captive mammals (McLaren *et al.* 2003) and is often attributed to crowded conditions (Moorhouse *et al.* 2007). The stress attributed to overcrowding was believed to be one of the reasons why released salmon conducted inefficient behaviours such as high general activity and poor habitat choice compared to wild salmon (Weber & Fausch 2003). A reduction in density can alleviate stress. For example, lowering density to more natural levels reduced stress in water voles (*Arvicola amphibus*) (Gelling *et al.* 2010). Intensively reared chickens exhibit less

severe pecking and lower mortality when reared in smaller, more natural densities (Nicol *et al.* 1999), however aggression also reduced when densities increased and exceeded natural densities (Nicol *et al.* 1999; Zimmerman *et al.* 2006).

1.5.4. Development of aberrant behaviour

Unnatural conditions and unnatural selection can have a major impact on development of maladaptive behaviours. In species that have had multiple generations in captivity genetic differences can arise between the wild and the captive populations. This could occur because of the lack of selection pressure from predation (Johnsson *et al.* 1996; Johnsson, Höjesjö & Fleming 2001; Sundström *et al.* 2005), or by human selection of traits that are advantageous to keepers and breeders (Kohane & Parsons 1988). The result is that behaviours will then start to fall outside the range of that exhibited in the wild and therefore individuals with these traits would quickly fail upon release (McPhee & Silverman 2004). For example, an important antipredator behaviour is the ability to detect predators, often achieved through vigilance behaviours (Elgar 1989; Roberts 1996; Caro 2005). This form of anti-predation combines an adaptive response to a fear and anxiety induced by perceived danger (Boissy 1995), but this is often not selected in captivity, where conditions tend to favour reduced emotional activity and increased tameness (Boissy 1995; Curio 1998; Price 1999; Rantanen *et al.* 2010). This could be exacerbated in the absence of predator controlled selection in captivity over generations (McPhee 2003; Kraaijeveld-Smit *et al.* 2006; Håkansson & Jensen 2008). This could be the reason why post release vigilance behaviour is less in released grey partridge (*Perdix perdix*) compared to wild partridges (Watson, Aebischer & Cresswell 2007; Rantanen *et al.* 2010). However the effect of domestication can be alleviated with more naturalistic conditions; captive gerbils (*Meriones unguiculatus*) had reverted towards the wild phenotype after one generation of rearing under a more naturalistic environment (Clark & Galef 1980).

1.6. Why a lack of studies conducted on animals for release?

There is an obvious lack of evidence of enhanced rearing conditions for animals destined for release into the wild. The reason for this is that many projects focus on rare and endangered species. Firstly, working with such species means there are often low sample sizes and a lack of replicable conditions required for detailed analysis, making more fundamental research difficult (Armstrong & Seddon 2008). Secondly, there may be a reluctance to attribute controls, or potentially costly treatments to rare species. Thirdly, it is difficult to follow the animals after release into the wild, with many programmes having poor and unfocused monitoring (Seddon, Armstrong & Maloney

2007), or insufficient project duration (Beck *et al.* 1994). In addition there is a reluctance to report failure (Sarrazin & Barbault 1996).

The solution is an analogous system that allows for large sample sizes, replicated conditions and adequate post release monitoring, where questions are identified *a priori*. Many of the issues identified in developing the science and directions of reintroduction biology can be addressed by with using game bird rearing as the model system, specifically the pheasant (*Phasianus colchicus*), red-legged partridge (*Alectoris rufa*) and the grey partridge.

1.7. The solution: the game rearing industry

1.7.1. The system: then and now

Pheasants were believed to have been introduced to Britain by the romans as early as the 4th century, certainly there were breeding populations in the wild in the 15th century (Hill & Robertson 1988j). Today, over 35 million pheasants and over five million partridges are released in the UK each year (PACEC 2008). These birds can either act to supplement a wild breeding stock of around 2.3 million birds (Gibbons *et al.* 1993), to create a breeding population (Aebischer & Ewald 2004; Buner, Browne & Aebischer 2011), or in some cases they are released with no intention of breeding and simply to act as targets for shooting. Therefore, by definition (IUCN 1998), these birds are released in a series of annual restocking events.

Artificial rearing of gamebirds for release has a long history (overview in Browne, Buner & Aebischer 2009). Originally these birds were nurtured by the protection of nests. As agricultural practice changed and natural populations declined, game keepers started to adopt the Euston System whereby natural nests were found and mapped by keepers and each day eggs were removed and replaced with artificial eggs. This process allowed the eggs to be placed under a more efficient broody hen, free from the high risk of predation, whilst the mother in the wild remained on the nest. Prior to hatching the eggs would be returned to the wild mother to be brooded. The Euston System was labour intensive and did not increase the population on the release site as it relied on the resident stock for eggs. More intensive methods became popular, whereby purchased eggs were incubated and brooded by hens in coops on rearing fields. When the chicks were eight weeks old, the chicks, the hen and the coop were placed into the wild where the hen and chicks would forage, after nine weeks the hen would be removed completely. This method, although labour intensive, would increase the stock on the estate for shooting.

Current methods maximise the numbers of birds that are able to be released by using mechanical incubators to hatch eggs and artificial brooders to intensively rear birds. Therefore parents or surrogate parents are not required. A hen can brood around 15 chicks whereas artificial brooders can brood up to 1000 chicks. The system uses a relatively barren and parasite free environment, *adlib* food provision, permanent warmth and shelter, medication from disease, fences to exclude predators, and mechanical "bits" to reduce the effects of aggression (Hill & Robertson 1988j; Buner & Schaub 2008; Ferretti *et al.* 2012). This process allows game-rearers to produce high numbers of "healthy birds" whilst adhering to DEFRA codes of practice (DEFRA 2009). These industrial methods can be adopted by researchers who can manipulate early rearing conditions, controlling for the physical environment including temperature, food availability, density and sex ratio. Sexes can be identified using morphological cues from one day old (Woehler & Gates 1970) and then can be marked using leg rings and patagial wing tags. Galliformes are robust birds that can tolerate reasonably high levels of handling from early life, allowing for experimental as well as observational studies to help understand mechanisms behind changes in morphology, behaviour and cognition (Madden & Whiteside 2013; Madden & Whiteside 2014).

Following captive rearing of around 6-8 weeks, pheasants are released initially into an open-topped pen. Release pens typically consist of a wire mesh fence around 2 m high enclosing an extensive area of woodland into which many hundreds, occasionally several thousands, of pheasants are released (GWCT 1991). The size of pens required using this system depends on the scale of the release and adherence to good practice, The Game and Wildlife Conservation Trust recommends 1000 or so pheasants per hectare of pen (Sage & Swan 2003). The primary function of the woodland release pen is to protect the young captive-reared birds from predators, in particular foxes, while they get used to roosting in trees or mature shrubs (GWCT 1991) over the first week or two following release. During this period they also provide a controlled environment for feeding and, if required, disease management (GWCT 1988; GWCT 1991). Birds then have free access to the wild where they live subject to ecological pressures. With the use of marking and monitoring strategies such as patagial wing tags, data loggers, and radio collars, individuals can be followed and their survival, movement, behaviour, reproductive success and fate can be assessed in a highly focused post release monitoring system of known individuals (Hessler *et al.* 1970).

Therefore the current rearing system of pheasants used by the shooting industry provides a novel but promising system to determine the effects of enhancing captive environments on post release survival. The system also provides an unusual opportunity to look at more fundamental aspects of reintroduction biology such as how individual behavioural differences within a released population can affect mortality and dispersal and how this can influence future population dynamics.

1.7.2. Released game birds in the wild: survival, reproductive success and developmental deficiencies

Released pheasants and partridges are incredibly unsuccessful. Released birds face four distinct threats post release. First, released birds are more vulnerable and therefore more likely to die from natural causes compared to their wild conspecifics, with hand reared birds being more vulnerable to predation than equally weighted wild birds (Hessler *et al.* 1970; Sage & Robertson 2000), Turner (2005) found 32% of released pheasants died in the first seven months of the year and a further 9.23% die after the shooting season prior to one year in the wild (See figure 1.1) (Hoodless *et al.* 1999). Some studies showing up to 70% of released pheasants (Brittas *et al.* 1992) and 72% of red legged partridges (Alonso *et al.* 2005) being predated in the first year. One factor for this susceptibility to predation is that captive reared birds exhibited lower individual vigilance levels compared to wild partridges (Watson, Aebischer & Cresswell 2007; Rantanen *et al.* 2010). An important anti-predation behaviour for ground dwelling galliformes is roosting at night (Wood-Gush & Duncan 1976), particularly against the crepuscular fox, the most prominent predator of released game (Robertson 1986). However, released grey partridge were often observed roosting in the field margins instead of the centre of a field (Dowell 1990) and released cheer pheasants (*Catreus wallichi*) were commonly found roosting on the floor instead of up trees (Garson, Young & Kaul 1992); both areas that have greater predation risk. Released pheasants tend to show less dispersal than wild pheasants (Bagliacca *et al.* 2010), remaining at a release site can attract predators (Banks, Norrdahl & Korpimäki 2002). Secondly, birds exhibit poor foraging ability and are unable to maintain body condition when released into the wild (Brittas *et al.* 1992; Sage & Robertson 2000). This results in birds developing a

high dependence on supplementary feeding which is commonly withdrawn in the spring, causing many individuals being unable to make the transition between the supplementary fed diets and a natural diet (Draycott *et al.* 1998). Females who breed during the spring often rapidly lose condition during this period, resulting in nest abandonment and even death sat on the nest (Robertson 1997; Hoodless *et al.* 1999). Female survival during the spring is lower for released birds (4%) compared to wild conspecifics (40%) (Musil & Connelly 2009). Thirdly, released birds show poor reproductive success. Socially the birds are unable to compete with wild birds, with males being continually harassed by wild birds and subsequently fail to breed (Anderson 1964; Brittas *et al.* 1992). This results in released males tending to have smaller harem sizes than wild pheasants (Hill & Robertson 1988a). Released females have lower incubation success (Leif 1994; Sage *et al.* 2003; Buner, Browne & Aebischer 2011), in some cases fledging only a quarter the broods, and producing one seventh of 12 week old chicks of wild conspecifics (Hill 1985; Hill & Robertson 1988a). Finally, released birds can be physiologically dissimilar to wild conspecifics, with reared pheasants being larger than wild birds (Bagliacca *et al.* 2010). Captive reared grey partridge had poorly developed flight muscles causing a shallower take off angle and reduced climbing rate compared to wild birds, making them more vulnerable to predation (Putaala *et al.* 1997). Captive reared grey partridge reared on a commercial diet often grew larger but with smaller hearts compared to wild birds (Putaala & Hissa 1995).

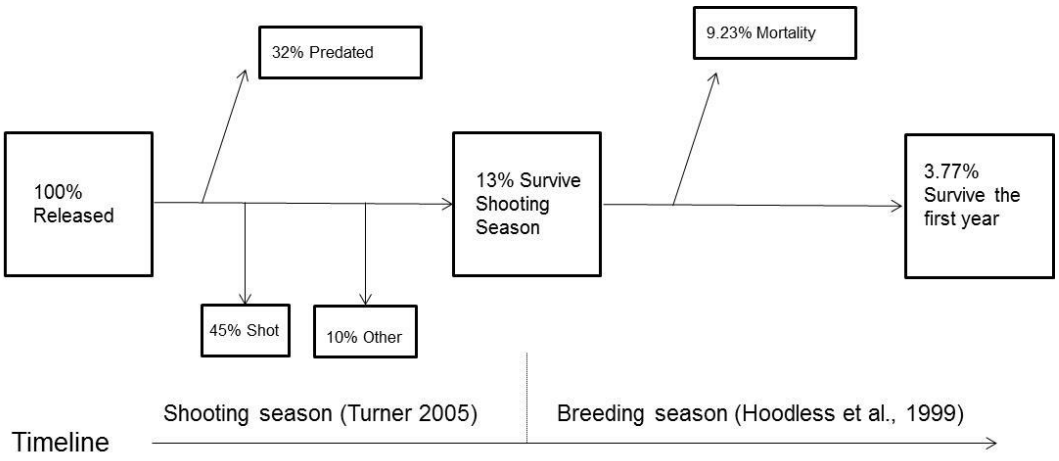


Figure 1.1. The percentage of mortality for the first year of a pheasant restocking programme.

Although captive-reared birds have low survival and reproductive success on release, their surviving wild offspring may be equally successful as their wild peers (Sage *et al.* 2003; Buner, Browne & Aebischer 2011), suggesting that physical and behavioural characteristics influenced by early life experiences are at fault rather than underlying genetic deficiencies.

1.7.3. Game birds: Developmental plasticity and manipulations to the rearing environment

Multiple aspects of the long term morphology and behaviour of galliformes are developmentally plastic, influenced by conditions experienced over short periods early in life. The mechanisms by which such differences may emerge can include the levels of steroid hormones in the egg which can affect wattle colour and other male sexual traits, digit ratio, patterns of female mate choice and male sexual behaviour (Romano *et al.* 2005; Rubolini *et al.* 2006; Rubolini *et al.* 2007; Saino *et al.* 2007; Bonisoli-Alquati *et al.* 2011a; Bonisoli-Alquati *et al.* 2011c; Rubolini *et al.* 2014). The diet that a bird experiences in its first few weeks of life affects its tarsal size and symmetry (Ohlsson & Smith 2001), male sexual ornaments (Ohlsson *et al.* 2002), body condition (Sage, Putaala & Woodburn 2002), body size (Orledge *et al.* 2012a), parasite load (Orledge *et al.* 2012b), and primary feathers development (Liukkonen-Anttila, Putaala & Hissa 2002). Such developmental plasticity is likely to have fitness consequences for released game birds that are artificially reared and released. However, only a few studies have utilised this developmental plasticity to investigate how the captive rearing environment can enhance develop characteristics that will aid post release survival.

The addition of a learned conspecific, in the form of a broody domestic chicken can cause released individuals to have better spatial behaviours and better antipredator behaviour, resulting in better survival compared to hand reared conspecifics (Buner & Schaub 2008; Gaudioso *et al.* 2011; Ferretti *et al.* 2012).

The provision of more fibre during early development caused red legged partridges to have heavier gizzards, longer intestines, smaller pectoral muscles, lighter spleens and lower plasma levels of proteins, glucose, cholesterol and triglycerides; these differences could have contributed to the observed lower survival after release compared to birds reared with commercial diet (Millán *et al.* 2003). The provision of an unpredictable food source caused grey partridges to survive better after release (Homberger *et al.* 2014) linked to better adaptation to an unpredictable post release environment in the form of boosted immune indices and glucocorticoid stress response (Homberger *et al.* 2013).

1.7.4. Advantages of environmental manipulations for the game industry

The result of this high mortality and poor reproductive success is that over 40 million game birds are released each year to supplement the wild population, in order to shoot around 14 million birds (PACEC 2008). This implies an accepted wastage of over 20 million birds. This prompts clear ethical, environmental and financial questions which demand answers.

Up to 25% of released pheasants die of natural causes in the first year (Turner 2004), therefore releasing birds that are ill prepared to survive in the wild is unethical.

Although game shooting provides positive environmental benefits from land management and supplementary feeding by enhancing biodiversity and increasing survival of non-game birds (Stoate 2002; Draycott, Hoodless & Sage 2008c), the scale and density of the release of game birds can also have detrimental effects on lowland habitats and ecosystems (Clarke & Robertson 1993; Sage, Ludolf & Robertson 2005).

By manipulating the current rearing environment to allow birds to develop the characteristic to survive in the wild would raise the ethical standard of the release programme. Releasing birds that are able to survive will mean fewer birds will be released each year, therefore reducing the impact on the environment. Such improvements in the survival of pheasants would not only reduce ethical and environmental costs, but could additionally provide the shooting industry with direct economic benefits. Currently it costs £13.76 to rear, release and maintain a bird

(SmithsGore & GWCT 2014). Reduced wastage of birds would therefore have substantial financial benefits to the industry.

1.7.5. What criterion is required for an adoptable and successful rearing regime?

It is important to determine is what is regarded as a successful target outcome. For many translocation programmes, success is determined when it reaches a certain criterion based on the creation of a self-sustaining population (Jule, Leaver & Lea 2008) (see 1.3). Ultimately a pheasant release programme would be truly successful if a self-sustaining population is created that is also able to maintain an economically viable harvest for the shooting community. Based on the numbers shot each year this seems far-fetched, therefore a revision of what determines a successful release needs to be evaluated. Perhaps here the ethical, financial and environmental aspects should be considered. If the proposed manipulations are able to increase survival of the released birds and therefore reduce the numbers required to be released each year for the same harvest, then it is feasible that we would reduce the cost of rearing, cost to the environment and improve the welfare of the animals upon release; this then could be determined as a success. With such high release numbers, even a 1% reduction in numbers released would equate to around 350000 birds.

Unlike highly focussed conservation programmes, rearing birds for sporting purposes differs because it works as a business on an industrial scale. Therefore manipulating the rearing conditions to promote survival is constrained by the industry itself and this could be the reason why we see little advances in the current system. Key to this is that to promote natural survival skills it is best to create a more naturalistic environment (Shepherdson 1994). However, natural environments expose wild animals to fear, stress and discomfort. Captive managers are responsible for welfare and the production of healthy animals during their time in captivity (Carlstead & Shepherdson 1994; Swaisgood 2007), therefore unlikely to adopt a system that would compromise welfare and perhaps place them at risk of prosecution. The application of a more naturalistic environment can also be highly time consuming and financially costly (Wallace 1994; Snyder *et al.* 1996), both factors not good for business. Finally, the shooting industry is predicated on the numbers of birds being shot, and therefore the risk of producing fewer shootable birds makes game breeders risk averse. Therefore, in order to create an adoptable system of rearing for the game-industry, the proposed environment should be cheap, easy and non-labour intensive to implement; it should not compromise welfare and should not affect the trade after release.

1.7.6. Benefits beyond the game industry

Although released pheasants and partridges are not endangered in the UK, they do however provide the ideal surrogate species for many other animals. Surrogate species are becoming an essential tool for understanding the problems with translocation programmes without the risk associated with manipulating the development of rare animals, for instance the Siberian polecat (*Mustela oversmanii*) has been used to replicate reintroduction techniques in the black footed ferret (Biggins *et al.* 2011), and the Andean condor (*Vulture gryphys*) has been used as a surrogate for the Californian condor (*Gymnogyps californianus*) (Toone & Wallace 1994). Pheasants and partridges can be surrogate species for many precocial bird species and more specifically galliformes. This is important because 44% of translocation programmes are conducted on birds (Fischer & Lindenmayer 2000) and up to 90% of programmes in the North America are conducted on game species (Griffith *et al.* 1989). Many galliformes are currently threatened and therefore the pheasant and partridge rearing system can provide the ideal surrogate for the malleefowl (*Leipoa ocellata*), the rusty-margined guan (*Penelope superciliaris*), the dusky-legged guan (*Penelope obscura*), the greater-sage grouse (*Centrocercus uro phasianus*), the sharp-tailed grouse (*Tympanuchus phaianellus*), and the white tailed ptarmigan (*Lagopus leucurus*) (WPA/IUCN 2009).

1.8. Conclusions and questions

Translocation programmes are typically highly unsuccessful. One explanation is the behavioural, physiological and cognitive deficiencies arising from suboptimal rearing facilities. However, these deficiencies can be mitigated with manipulations to the rearing environment. I have highlighted why developmental deficiencies occur during rearing, stating that absence of a parent or learned companions, a barren environment, lack of a predatory stimulus, a non-natural diet and stress are all crucial factors. I also show that there are very few studies looking at how enhancements to the captive environment can impact post release survival. It is important to not look at behavioural, physiological and cognitive development separately because many survival skills rely on a complex interaction between the three disciplines. Therefore, I will take a holistic approach to determine how simple and cost effective manipulations to early rearing conditions can have wide ranging consequences, influencing behavioural, physiological and cognitive development in pheasants, an animal used in many annual high-number restocking events.

Chapter two will address the issue of non-natural diet and how an unnatural diet, even though of nutritional equivalence to a natural diet might: 1) reduce the

chances of learning discrimination skills; 2) result in a gastro-intestinal system less able to cope with natural diet; 3) not influence the development of important handling techniques; and crucially 4) culminate in affecting post release behaviour and survival. The goshawk and the buzzard are key predators for released pheasants (Kenward, Marcström & Karlbom 1981; Kenward *et al.* 2001) and will predate whilst the pheasants are foraging in the open field. Therefore, I am interested in specific characteristics that will aid survival during these periods; such as post release foraging duration and vigilance levels. Poor foraging behaviour, diet choice and gut morphologies and are a major cause of post-release mortality (Draycott *et al.* 1998; Draycott 2002) and therefore I am interested in foraging efficiency, post release diet composition and gut morphology.

Chapter three will address the issue of a structurally barren environment. I will manipulate the pheasant rearing environment by adding structures to allow the development of perching behaviour. I will assess if these conditions affect: 1) the propensity for a bird to perch; 2) the physiological characteristics that will aid the birds to access and remain on a perch for an extensive period of time; 3) spatial ability in cognitive tests; 4) the post release behaviour and survival. The fox is major predator for released pheasants, particularly during the crepuscular hours (Brittas *et al.* 1992) and elevated roosting at night is a method wild chicks use to reduce the risk of predation (Wood-Gush & Duncan 1976). I am specifically interested in post release use of elevated perching and the physiological mechanisms that aid this behaviour. In addition I am interested in the individual's spatial memory which can be improved if reared in more complex environments (Wichman *et al.* 2007).

The review has highlighted the need to maintain a sufficient level of welfare, as stress can compromise development and impact post release disease resistance. The IUCN state that the welfare of animals is paramount concern through all stage of a reintroduction programme (IUCN 1998), however few conservation biologists are equipped with the scientific tools needed to looking closely at welfare and there is little interaction between welfare researchers and conservation biologists (Teixeira *et al.* 2007). In **Chapter four**, I will use behavioural indicators such as aggression, preening and stereotypies as well as mortality to: 1) determine how enrichment introduced with the primary aim of improving post release survival impacts welfare of the pre-release animal; and 2) add to a very small literature of pheasant welfare.

Personality is becoming a vast and important area of animal behaviour and is now growing in the field of conservation biology. However, there is little evidence of how personality of animals released in high numbers can influence mortality and survival. In **Chapter five** I will assay the personality of a large number of juvenile pheasants before release and follow their fate during the first eight months of their reintroduction. I will use the same testing equipment and behavioural assays that have previously showed to be individually consistent across time in pheasants (Madden & Whiteside 2014). I will specifically test whether those dying of natural causes differ in their personality compared to the original population personality mean. I will ask if personality relates to dispersal. Finally I will ask if personality as a juvenile influences the development of morphological characteristics which might affect future reproductive success. From this I hope to provide advice on potential manipulation either to the release group dynamics or to the environmental factors within the release site to help establish a population that contains multiple personality types.

Having focused predominantly on mortality and dispersal after release, released pheasant also exhibit poor reproductive success (Brittas *et al.* 1992; Sage & Robertson 2000). Although there is a vast literature on pheasant natural history and the history of sexual systems (Ridley 1983; Ridley & Hill 1987), identifying that males are territorial and provide no parental care (Taber 1949) and that female predominantly choose males based on morphological features and not territory quality (von Schantz *et al.* 1989d; Göransson *et al.* 1990; Grahn, Göransson & von Schantz 1993a), there is a distinct lack of research on harem defence polygyny and social factors relating to reproductive success. In **Chapter six** I will use behavioural observations of wild pheasants to try to understand why observed harem sizes are skewed towards the small even though theory suggests that females should aggregate around a small number of highly sexually successful males. Future research could build on these preliminary observations to determine if differences in physiology, morphology and cognition that are attributed to manipulations to early developmental rearing environment can have longer term fitness consequences.

The entire study will take place over three years and will consist of two rearing seasons during which I will have control over the early rearing environment. In each year I will rear 900 birds. These birds will be obtained from a commercial supplier at one day old and randomly assigned to an experimental treatment. In 2012 I will have two treatments only differing in supplementation of diet (see **Chapter Two**). In 2013 i will use a 3x2 design with two dietary treatments and three treatments differing in a population's access to perches (see **Chapter Three**). Analyses for chapter two will

include birds reared in both years of the study. Chapter three will only include birds that were reared in 2013. All behavioural tests and observations that will be conducted for chapter four (welfare) and chapter five (personality) will be from the same populations as those in **Chapter Two** and **Chapter Three**. These birds will remain under controlled environments for six weeks after which I will release them into the wild (see 1.7.1). I am interested in behaviours, physiology, fate and dispersal of birds in the wild and these data will be collected in conjunction with a commercial shoot and detailed field observations. **Chapter Six** will be based on birds from the broader population on the estate and may include birds which I did not rear.

My final chapter, **Chapter seven**, will synthesise my work and draw together the conclusions from my study, from these I will discuss how they add to the current knowledge of captive-rearing and release, and examine the wider implications of my results from the pheasant rearing system for reintroduction biology. I will calculate the likely costs of interventions and try to extrapolate the potential economic and environmental benefits of implementing changes to the current methods of rearing.

Chapter Two

Diet complexity in early life affects survival in released pheasants by altering foraging efficiency, food choice, handling skills, and gut morphology

ABSTRACT

Behavioural and physiological deficiencies are major reasons why translocation programmes suffer from high mortality when captive animals are used. Mitigation of these deficiencies is essential for successful reintroduction programmes.

Our study manipulated early developmental diet to better replicate foraging behaviour in the wild. Over two years we hand reared 1800 pheasants (*Phasianus colchicus*) from one day old, for seven weeks under different dietary conditions. In year one, 900 pheasants were divided into three groups and reared with (i) commercial chick crumb, (ii) crumb plus 1% live mealworm or (iii) crumb plus 5% mixed seed and fruit. In year two, a further 900 pheasants were divided into two groups and reared with (i) commercial chick crumb or (ii) crumb plus a combination of 1% mealworm and 5% mixed seed and fruit. In both years the commercial chick crumb acted as a control treatment, whilst those with live prey and mixed seeds and fruits mimicking a more naturalistic diet. After seven weeks reared on these diets pheasants were released into the wild.

Post release survival was improved with exposure to more naturalistic diets prior to release. We identified four mechanisms to explain this. Pheasants reared with more naturalistic diets: 1) foraged for less time and had a higher likelihood of performing vigilance behaviours; 2) were quicker at handling live prey items; 3) were less reliant on supplementary feed which could be withdrawn; 4) developed different gut morphology.

These mechanisms allowed the pheasants to: 1) reduce the risk of predation by reducing exposure time whilst foraging, while allowing more time to be vigilant; 2) be better at handling and discriminating natural food items, and not be solely reliant on supplementary feed; 3) have a better gut system to cope with the natural forage after the cessation of supplementary feeding in the spring.

Learning food discrimination, preference and handling skills by the provision of a more naturalistic diet is essential prior to the release of pheasants in a reintroduction program. Subsequent diet, foraging behaviour, gut morphology and digestive capabilities all work together as one nutritional complex. Simple manipulations during early development can influence these characteristics to better prepare an individual for survival upon release.

2.1. INTRODUCTION

Captive reared animals released as a result of reintroduction programs suffer from extremely high mortality (Kleiman 1989; Snyder *et al.* 1996); significantly higher than their wild conspecifics (Fischer & Lindenmayer 2000). One cause may be due to the genetic differences between wild and captive reared individuals, which can arise if a small founder population in captivity are highly inbred or genetically adapted to conditions different to those found at the site of release (Armstrong & Seddon 2008). However, although released animals commonly have low survival and reproductive success, their surviving wild offspring are often equally successful as their wild peers (Sage *et al.* 2003), suggesting that physical and behavioural characteristics influenced by early life experiences are at fault (Snyder *et al.* 1996; van Heezik & Seddon 1998). The effects of rearing conditions can be profound during the early stages of development (Desai & Hales 1997; Latham & Mason 2008) and can persist after independence (Cam, Monnat & Hines 2003), influencing adult survival and reproduction (Lindström 1999). When an individual is subjected to unnatural or artificial rearing conditions prior to release they may lack opportunities to acquire essential survival skills such as predator detection and avoidance (Kleiman 1989; Griffin, Blumstein & Evans 2000), food acquisition and processing (Ellis *et al.* 2000), social behaviour (Fleming & Gross 1993) and locomotion (Hill & Robertson 1988j). These behavioural deficiencies may be an important reason for the high mortality and poor success of reintroduction programmes (Kleiman 1989; Fischer & Lindenmayer 2000). The continued low success rates found in reintroduction programmes has prompted calls for a more concerted effort to understand the cause of behavioural deficiencies and to develop ways of mitigating their impact (Kleiman 1989; Seddon, Armstrong & Maloney 2007). However, the nature of reintroduction programmes, focussing on rare and endangered species, often makes more fundamental research difficult and can have poor monitoring (Armstrong & Seddon 2008), insufficient project duration (Beck *et al.* 1994) and a reluctance to report failure (Sarrazin & Barbault 1996). Furthermore,

recovery programmes can lack the sample sizes to allow for controlled and replicable conditions required for detailed analysis (Armstrong & Seddon 2008). In order to investigate the effects of early rearing conditions it is necessary to use a system in which large numbers of individuals can be reared under a range of controlled conditions, and their survival accurately monitored post-release.

Pheasants (*Phasianus colchicus*), reared and released in the UK for recreational shooting, offer an introduction program that avoids such confounds and complications found with work on endangered species, with vast numbers of individuals being used each year offering a unique opportunity to investigate the role of early rearing on behavioural development and the consequent fate of introduced birds. Up to 35 million birds are released each year to supplement wild stock for shooting (PACEC 2008) and typically around 25% of released birds die in the 3 to 4 month period after release and before shooting begins (Turner 2004). Wild-born pheasants show better survival compared to those reared and released birds (Hill & Robertson 1988j; Brittas *et al.* 1992; Leif 1994). Pheasants face three distinct threats post release. First, released pheasants are more vulnerable to predation than their wild conspecific (Hessler *et al.* 1970; Sage & Robertson 2000). Second, birds are unable to maintain body condition when released into the wild, which is often attributed to poor foraging efficiency after release (Brittas *et al.* 1992; Sage & Robertson 2000). Third, birds may develop a high dependence on supplementary feeding which is commonly withdrawn in the spring and are often unable to make the transition between the supplementary fed diets and more a natural diet (Draycott *et al.* 1998).

We concentrated on the diet that chicks experienced early in life, and asked how simple supplementation of standard, homogenous commercial rearing feed may provoke complex and long lasting behavioural and physiological developments that impact on the fate of the released birds. Pheasants are naturally omnivores, utilising a wide range of food items (Hill & Robertson 1988j). Pheasants typically follow their mother to sites to learn about food (Hill 1985). Captive rearing may inhibit individual

opportunities for learning and exposure to different food types. This likely impacts on two mechanisms pertaining to diet which may influence individual chances of survival upon release: increased foraging efficiency and increased dietary breadth.

Developing an efficient foraging technique means that a bird can ingest more food, increasing their body condition, and in addition spend less time foraging in risky locations exposed to predation. Foraging efficiency can be increased by improving food handling skills. This increased efficiency allows greater effort to be allocated to predator detection, an activity which is mutually exclusive to foraging for a ground-feeding bird. Pheasants are highly susceptible to aerial predation from buzzards, *Buteo buteo*, and Goshawks, *Accipiter gentilis* (Kenward, Marcström & Karlbom 1981; Kenward *et al.* 2001). Therefore, we predict that birds given early exposure to a more complex diet, including live prey, will; a) develop more efficient prey handling skills; b) spend a shorter proportion of their time foraging, allocating more time to vigilance behaviours; and consequently c) survive for longer post-release.

Increasing dietary breadth becomes paramount with the withdrawal of supplementary feeding, permitting a full transition to the wild life. An inability to identify novel food items when supplementary feeding is stopped is one of the main reasons why pheasants suffer from loss of condition during the spring (Draycott *et al.* 1998; Draycott 2002). Food discrimination and dietary preference are important learned components of foraging behaviour (Kitchener 1999). Restricting access to a wide diet due to use of homogenous commercial rearing feed early in life may inhibit individual opportunities for learning and experience. A homogenous, or narrow, diet is also likely to detrimentally affect gut development and nutrient processing. The gut is highly plastic and changes with diet (Leopold 1953; Moss 1972), and these changes affect digestive ability (Milne *et al.* 1978). Avian species are precluded from simply enlarging gut size due to the energetic costs of flight increasing disproportionally to mass (Dudley & Vermeij 1992). This trade-off between flight and digestion means that bird guts are highly plastic. In gallinaceous birds (e.g., capercaillie (*Tetrao urogallus*) and red grouse

(*Lagopus lagopus*)), individuals that eat coarser, more fibrous food have bigger guts (Moss 1972; Putaala & Hissa 1995). This has fitness consequences, with abnormal gut development suggested as one reason for poor grey partridge survival after release (Putaala & Hissa 1995). Such ability to efficiently process a broad diet, especially for omnivorous pheasants, is crucial, especially after the cessation of supplementary feeding. Therefore, we predict that birds given early exposure to a more complex diet will; a) utilise a broader diet and be less reliant on artificial supplementary feeding; and b) develop a gut morphology better able to absorb a complex diet.

We experimentally manipulated early life diet in two years by supplementing uniform food with living prey and wild bird seen and fruit across different experimental groups. In the first year we tried to isolate prey handling skills from increased dietary breadth. In the second year we combined the two treatments. We monitored survival of individuals in the wild and then through experiments conducted in captivity and observations after release into the wild we tested the four mechanisms to explain differences in survival. We predict that uniform, unnatural food, even though supplying a sufficient balance of nutrients to facilitate growth and development: 1) reduces the chances of learning discrimination skills and therefore reduce dietary breadth; 2) such a diet will result in a gastro-intestinal system less able to cope with natural diet; 3) important food handling skills are not learned; and crucially 4) the improper development of such skills will affect post release behaviour and survival.

2.2. METHODS

2.2.1. Rearing and release into the wild

We reared and released pheasant chicks in the late spring/early summer of 2012 and 2013 on the Middleton Estate, Hampshire. The estate hosts a game shoot and employs two gamekeepers to manage the release of pheasants through habitat management, providing supplementary food, and controlling predator numbers. In each

year, we purchased nine hundred one day old pheasants from a commercial supplier. Chicks were marked using individual numbered plastic patagial wing tags (Roxan Ltd) and randomly allocated to treatment groups. In 2012 we applied three dietary treatments each with 10 replicate groups, with each group comprising 30 birds, thus rearing 300 birds in each treatment. In Treatment 1, a control, chicks were reared on standard rearing crumb. In Treatment 2, chicks were reared on the standard crumb with additional 5% commercial mixed seed (Premium wild bird seed mix composing of wheat, cut maize, black sunflower seeds, naked oats, red dari, kibbled peanuts, yellow millet, white dari, red millet, pinhead oatmeal, canary seed, safflower seed, hempseed and raisins). In Treatment 3, chicks were reared on standard crumb with additional 1% live mealworms. In 2013 we applied two dietary treatments each with 15 replicates of 30 chicks. In Treatment 1, a control, chicks were reared on standard rearing crumb. In Treatment 2, chicks were reared on standard chick crumb plus a combination of the supplements from 2012, with mealworms (1%) and mixed seed supplement (5%). All chick crumbs were commercial (Sportsman game feeds), age appropriate and provided *ad lib* and in excess. Water was available *ad lib*.

Each group of chicks (n = 30) were housed separately in a heated shed (1.3m x 1.3m) for the first two weeks and for the next five weeks they had access to an open grass run (1.3m x 6.8m) as well as the shed. Birds were in visual but not auditory isolation from other replicates throughout. To maintain stocking density, any bird that died during the rearing period was replaced by a sex-matched individual. Replacement chicks were excluded from subsequent analyses. In addition, in 2013, we also reared a further 60 birds, in two pens, on standard rearing crumb with additional 1% dead mealworms.

At the age of seven weeks, the birds from all treatments were mixed together and placed into one of two open top release pens on the estate. Release pens typically consist of a wire mesh fence around 2 m high enclosing an extensive area of woodland

into which many hundreds, occasionally several thousands, of pheasants are released (GWCT 1991). The size of pens required using this system depends on the scale of the release and adherence to good practice, The Game and Wildlife Conservation Trust recommends 1000 or so pheasants per hectare of pen (Sage & Swan 2003). Our pens measured ~1.4Ha and 1.0Ha and contained 360 and 540 of our birds respectively, along with around 500 birds that had been commercially reared. The primary function of the woodland release pen is to protect the young captive-reared birds from predators, in particular foxes, while they get used to roosting in trees or mature shrubs (GWCT 1991) over the first week or two following release. During this period they also provide a controlled environment for feeding and, if required, disease management (GWCT 1988; GWCT 1991). Our pens contained water and food *ad lib*. Birds could disperse at will from the pen and were free to roam and mix with other pheasants released on the estate for recreational shooting. The shooting season lasted from the beginning of October until February.

2.2.2. Measuring survival in the wild

We counted the number of birds that survived the first year using three methods of recovery: 1) live birds were spotted on the estate from a distance using binoculars and identified using their patagial wing tags (2 birds); 2) in the second shooting season we recorded the number of year one birds that were shot, therefore over 17 months old and having survived a potential breeding season (19 birds); 3) we recorded the number of year one birds caught during an intensive trapping regime run between 14 February and 20 March 2014, meaning that any such caught birds were at least 21 months old and had survived a potential breeding season. The trapping regime used baited funnel traps to capture tagged pheasants. Traps were checked three times a day (1 bird). Because the numbers from each sampling method were small we combined the total number of birds observed using the above methods and we used binomial tests to ask whether survival differed across rearing treatments. For birds released in 2013 we

were only able to obtain survival data from birds that were shot in the 2014/15 shooting season, and thus birds that were over 18 months old (18 birds). We also recorded the number of birds that died of natural causes prior to the start of the first breeding season by searching the estate and surrounding areas. Post release and prior to the hunting season (June -October) we conducted daily searches of areas of the estate. During the hunting season (October-February) the area was visited less frequently but more methodically as beaters, engaged in driving the game towards the waiting guns, were informed of the project and searched for carcases and tags as they walked through the estate. After the shooting season (March-June) the same area was visited about once a week.

In order to test whether rearing condition affected adult body mass, we collected all shot birds and weighed them (Slater Super Samson spring balance – precision 5g) within four hours of death. In addition we weighed all birds that were caught during the month of trapping (February-March 2014). This ensured that any differences in mass across treatment were not due to differing propensities to be shot, with lighter birds being likely to fly higher and perhaps be more likely to be shot at (Robertson, Wise & Blake 1993).

2.2.3. Measuring dispersal from the estate

Neighbouring estates and shoots were informed of the study and released pheasants that were shot outside of the estate were returned to us. Unfortunately the inevitable delay in returning carcasses meant that we were often unable to conduct *post mortem* analyses on these birds. We used a chi-square test to ask whether birds that dispersed and were shot off the estate differed across rearing treatment.

2.2.4. Measuring foraging and vigilance behaviour in the wild

In 2012, we collected continuous focal follows from 167 released pheasants, individually identified by their patagial wingtag, between 18 September 2012 and 5 November 2012. We recorded the total time observed, the time spent foraging and the number of foraging bouts they performed. A foraging bout began on the lowering of the head and neck towards to the ground and ended when the head and neck rises again. Time dedicated to a behaviour, such as vigilance, reflects the prey's perception of predation risk (Roberts 1996; Mooring *et al.* 2004). Vigilance may vary depending on protective cover (Barnard 1980; Caraco, Martindale & Pulliam 1980) therefore we recorded the extent of protective cover as "closed" if the focal bird was in an area offering protection from an aerial attack in the form of bushes and trees, and as "open" if there was absence of such protection (e.g. open field). It was only possible to observe birds in habitats that allowed a prolonged viewing window with vegetation lower than the height of the birds. We also considered the time of day when observations were made, as this may correspond to differences in levels of hunger or exposure to predators (Rantanen *et al.* 2010). Observations were conducted from a vehicle to reduce disturbance. Between 15 August 2013 and 16 September 2013 we repeated the continuous focal follow procedure on 213 pheasants reared and released in 2013; this allowed us to collect event behaviours such as foraging time and the number of foraging bouts. At the same time, on the same focal individual, we conducted an instantaneous point sampling procedure at 30 second intervals; this allowed us to collect state behaviours, enabling us to create an activity budget.

Wild foraging percentage was calculated from data collected in the continuous focal follows conducted in 2012 and 2013, and normalised using a logit transformation: log (y/1-y) (Warton & Hui 2010) and general linear model used (GLM). For vigilance likelihood, recorded using the instantaneous point sampling procedures in 2013, we used a generalised linear model (GLZM) with a binary distribution and a probit link

function. In both models sex, early rearing environment, time of day and cover were fixed factors, including all two-way interactions. All models were visually inspected to ensure homogeneity of variance, normality of error and linearity. *Post-hoc* pair-wise comparisons were conducted on all significant results and reported. A GLM was used to determine difference of mass between treatments controlling for the age of the bird.

2.2.5. Experimentally measuring food handling skills

In 2012, we presented 117 four week old chicks, randomly chosen from each treatment (Mealworm = 39, Mixed-seed = 39, Control = 39) with a food handling test. A cricket (*Gryllus assimilus*), a novel insect that could be eaten, was tethered on a 20 cm line and concealed by a barrier connected to a pulley system. Pairs of individuals were randomly selected and placed into the arena (1.30m x 1.30m). Pairs were essential because preliminary work showed that singly tested pheasants were too stressed to forage. After a five-minute habituation period the observer remotely exposed the cricket. Both birds were observed during the test. Time of detection of the cricket was recorded for both birds. Pheasants like any avian species with laterally placed eyes will first turn their head sideways to inspect food (Bischof 1988; Hodos 1993), so we used this behaviour as a measure of first detection. We then measured the time it took for the complete consumption of the cricket by one of the birds. All statistical analyses were based on one bird from each pair to ensure independent results. We subtracted the time of first detection from the time of consumption for the analysis to obtain handling time. In 2013 we conducted the same experiment on birds reared with the mixed diet (n=25) and birds from the control diet (n = 21). In addition to the two rearing groups, we reared 60 pheasants supplemented with dead mealworms and a sample of these (n = 14) were tested to determine if the movement of the prey was required to enhance foraging performance, or simply a prior ingestion of an insect. This control also determined if a simple nutritional advantage from eating mealworms led to better

foraging efficiency. We used a Kruskal-Wallis test to explore differences in handling time between rearing treatments.

2.2.6. Measuring diet choice in the wild

In 2013, we emptied the crop of 168 shot birds and identified and quantified its contents by (i) recording the mass of all keeper-supplemented food items (wheat, barley and maize) and (ii) recording the number of non-supplemented food types (e.g. grass, insects, galls and wild seeds). We used a Mann-Whitney-U test to explore differences between rearing treatment and the number of non-supplied food types and the mass of supplementary food items found. We determined which birds were completely reliant on food provided by the game keeper indicated as having crops containing only supplementary feed. We also determined which birds were completely independent of game-keeper provision indicated by a crop sample with no supplementary feed. Birds with empty crops were excluded from the analysis. We used chi-squared tests to ask whether rearing treatments differed in the number of pheasants with a crop content indicating complete reliance on supplementary feed or if they differed in the number of pheasants entirely independent of supplementary feed.

2.2.7. Measuring gut morphology

We measured gut morphology of 186 birds shot in 2012. Each bird was weighed within four hours of being shot and linear gut measures (crop height, length and width; crop to gizzard, proventriculus, gizzard height, length and width, intestine length, ceca length 1, ceca length 2) were taken after removing mesenteries (for methods see Leopold 1953). These linear measures were divided by an individual's mean tarsus length to correct for body size. We used principle component analysis (PCA) with an oblimax rotation to collapse the 11 linear measurements, and extracted components with Eigen values >1. A MANOVA was conducted on the extracted components with the sex and rearing treatment as fixed factors.

2.2.8. Ethical note

All birds were reared using commercial procedures that adhere to the DEFRA Code of Practice for the Welfare of Gamebirds Reared for Sporting Purposes (DEFRA 2009). For all behavioural testing, two birds were tested together to reduce stress, and all birds were only tested once. Released birds were attended by a game keeper. Once birds dispersed from the release pen, the keepers supplied supplementary feed and water, which was reduced after the shooting season (from 1st February). The birds were shot as a part of a commercial shoot, and were not specifically shot for this study. The work was approved by the University of Exeter Psychology Ethics Committee and conducted under Home Office licence number PPL30/2942.

2.3. RESULTS

2.3.1. Survival

In 2012, more birds reared with complex diets were detected as having survived for a year in the wild than control birds ($\chi^2 = 6.45$, $p = 0.031$, Figure 2.1a). We detected a similar trend in 2013 when the dietary conditions were combined ($\chi^2 = 3.56$, $p = 0.059$, Figure 2.1b). The rearing treatment did not affect the numbers of birds that were shot ($\chi^2 = 1.00$, $p = 0.61$) or the numbers of birds dispersing from the estate ($\chi^2 = 1.51$, $p = 0.47$) during the first year after release into the wild. We found that the number of birds dying of natural causes prior to the end of the shooting season did not differ between treatments (2012: $\chi2 = 0.48$, $p = 0.78$; 2013: $\chi2 = 0.89$, $p = 0.34$).

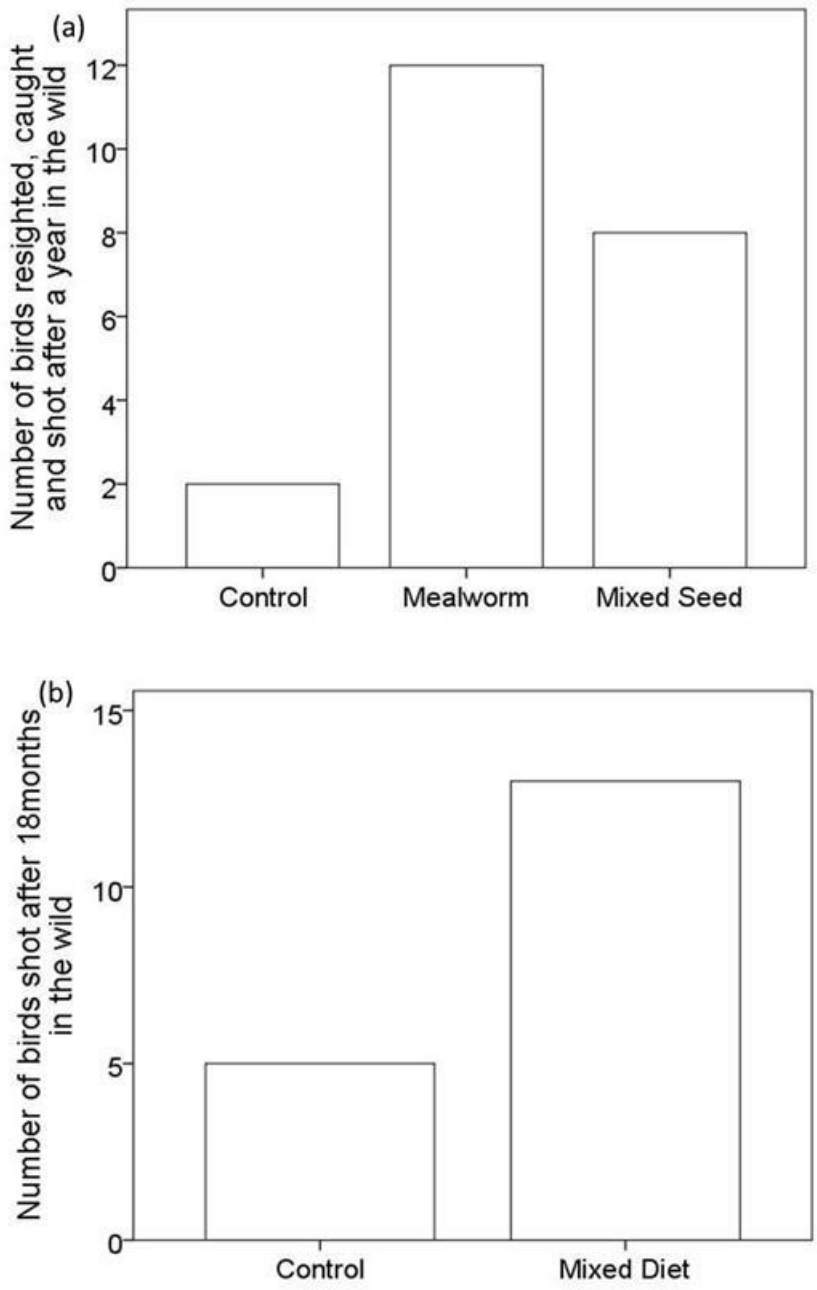


Figure 2.1. The number of birds a) reared in 2012 and resighted, shot or trapped during the following year, according to their different rearing environments; and b) reared in 2013 and shot during the 2014 shooting season after 18 months in the wild.

2.3.2. Foraging and vigilance behaviour in the wild

In 2012, individuals from the control treatment spent 12.3% longer foraging when in the wild than those reared in with supplementary mixed seed diet (post hoc test: p = 0.007) and 13.3% longer foraging than those reared with supplementary

mealworms (post hoc test: p = 0.001) (GLM: Treatment: $F_{2,145}$ = 4.24, p = 0.016, Figure 2a). Likewise, in 2013, control individuals spent 26.7% longer foraging when in the wild than birds reared with the mixed diet (GLM: Treatment: $F_{2,186}$ = 17.90, p < 0.001, Figure 2b). Birds reared with the mixed in 2013 spent 33.9% longer being vigilant than the control group (GZLM: Treatment: X_1 = 99.39, p < 0.001, Figure 3). These differences were not explained by time of day (2012: $F_{1,145}$ = 3.81, p = 0.053; 2013: $F_{1,186}$ = 0.63, p = 0.43) or level of cover in which the bird was observed (2012: $F_{1,145}$ = 2.93, p = 0.089; 2013: $F_{1,186}$ = 1.78, p = 0.183). All interactions did not have a significant effect on the model.

This difference in foraging time between treatments did not alter mass gain. After a period of 4-7 months in the wild, birds shot during the shooting season showed no differences in mass across treatments (2012:GLM: Treatment: $F_{2,208}$ = 0.80, p = 0.45; 2013:GLM: Treatment: $F_{1,107}$ = 0.63, p = 0.43). The birds that were caught alive during the breeding season, after a period of 8-10 months in the wild also showed no difference in mass across treatments (GLM: Treatment: $F_{1,27}$ = 0.01, p = 0.91).

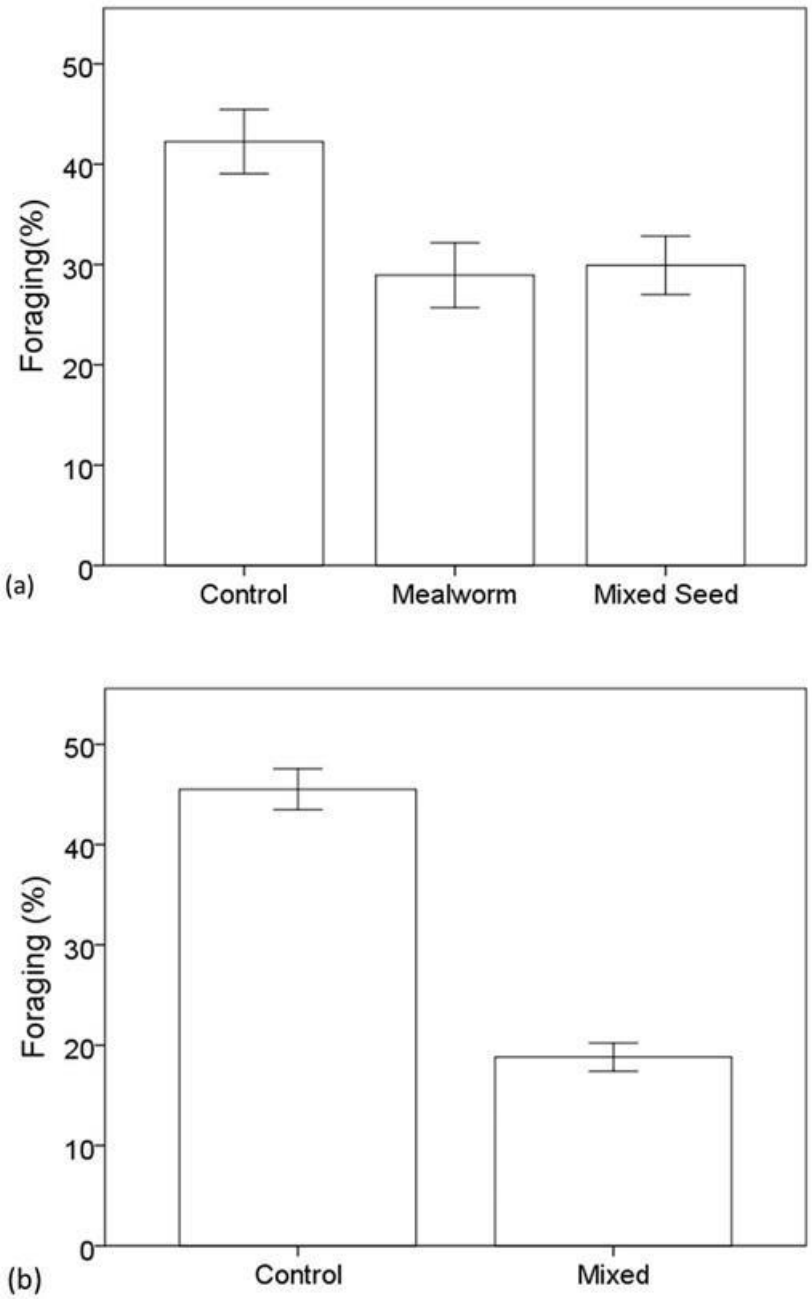


Figure 2.2. The mean percentage of time spent foraging in the wild by a bird reared under differing environments in; a) 2012; b) 2013. Error bars indicate ±1SE.

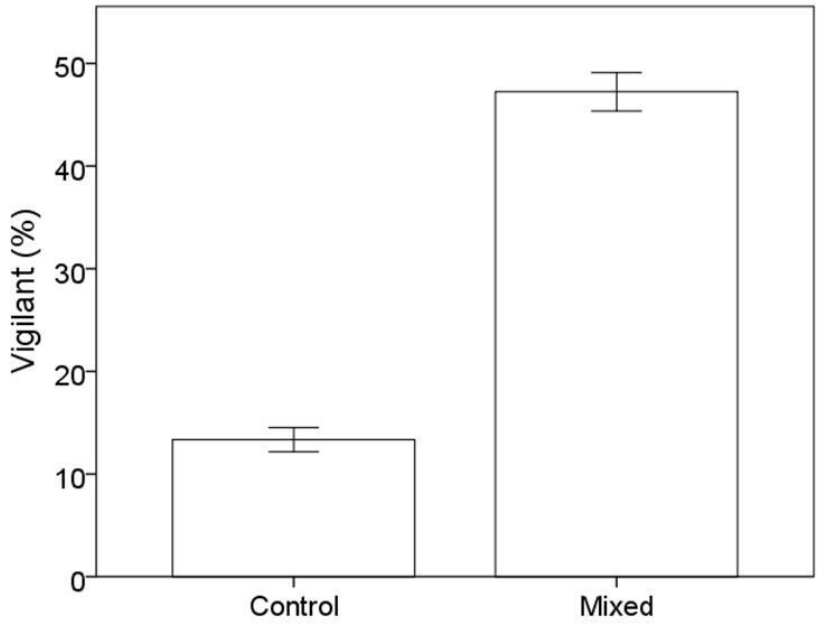


Figure 2.3. The mean percentage of time spent being vigilant in the wild by a bird reared under differing environments in 2013. Error bars indicate ±1SE.

2.3.3. Food handling skills

In 2012, birds reared with mealworms were more than twice as fast at catching and eating the tethered crickets after detection than those reared with supplementary mixed seed (post hoc test: $p = 0.003$) or the controlled diets (post hoc test: $p = 0.003$) (Kruskal-Wallis: $H(2) = 14.59$, $p = 0.01$, Figure 2.4a). There was no difference in the amount of time it took to detect the cricket between treatments (Kruskal-Wallis: $H(2) = 1.02$, $p = 0.60$). In 2013, we found that birds reared with live mealworms were quicker to eat the cricket after detection than both the birds reared with dead mealworms (post hoc: $p = 0.001$) and those reared with the controlled diet (post hoc: $p = 0.004$). Birds reared with dead mealworms showed no difference in their ability to consume a cricket after detection than birds reared without mealworms (post hoc test; $p = 0.39$) (Kruskal-Wallis: $H(2) = 14.51$, $p = 0.001$, Figure 2.4b).

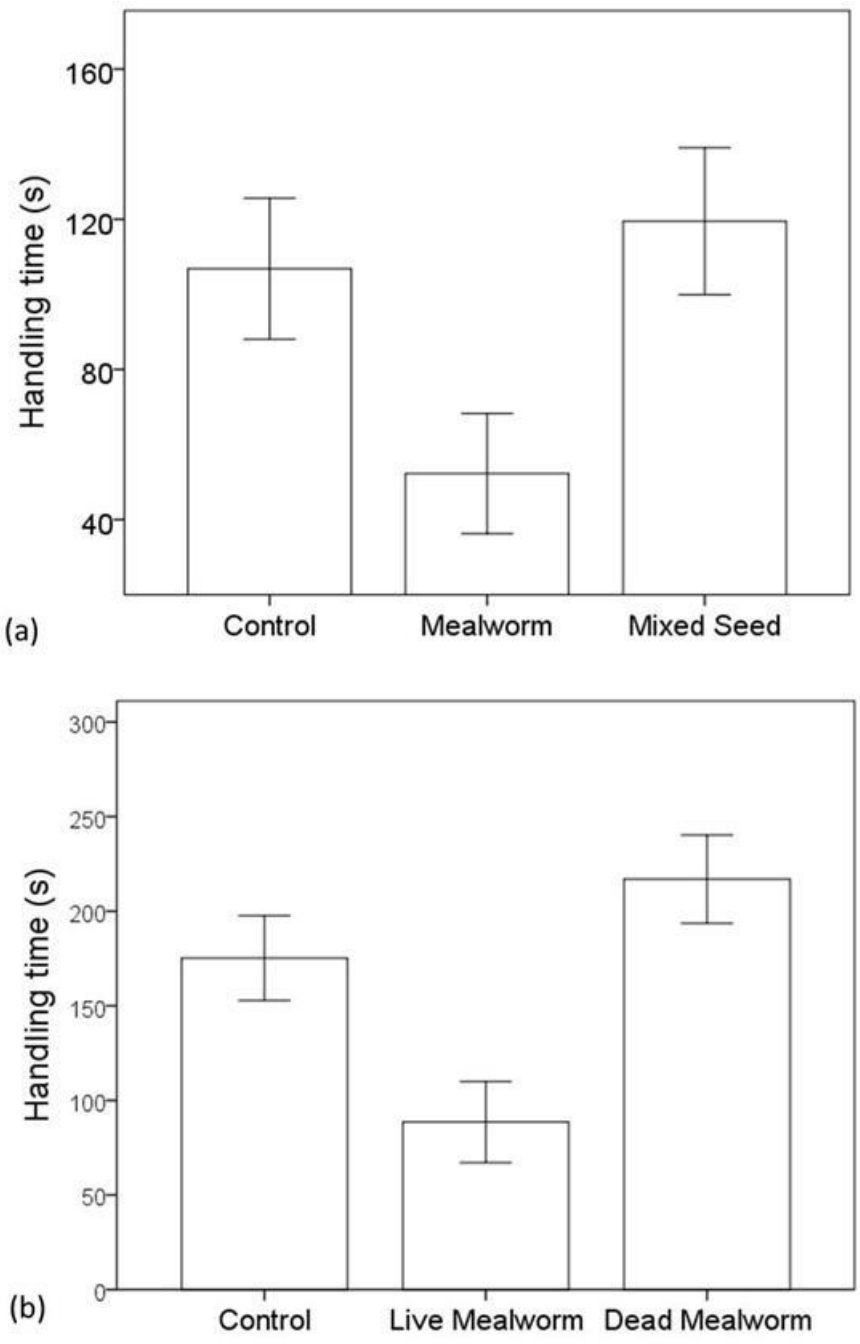


Figure 2.4. Time taken for a focal chick reared with one of three diets to eat a live cricket once it had been detected in a) 2012, and b) 2013. Error bars indicate ±1SE.

2.3.4. Diet choice

The mass of supplemented food (maize, wheat and barley) found in the crop of birds shot in 2013 did not differ with their rearing treatment (U_{168} = -1.14, p = 0.25). However, the birds reared with the mixed diets had higher numbers of non-supplied

food types in their crop compared to birds reared with the control diets ($U_{168} = 2.51$, $p = 0.012$, Figure 2.5). There were disproportionately more birds reared with the control diet (19) completely reliant on supplementary food items than birds reared with the mixed treatments (5) ($\chi^2_{(1)} = 8.17$, $p = 0.004$). Birds from the mixed group (12) tended to be more likely to be completely independent of keeper provision than the birds reared in the control environment (5), ($\chi^2_{(1)} = 2.88$, $p = 0.09$).

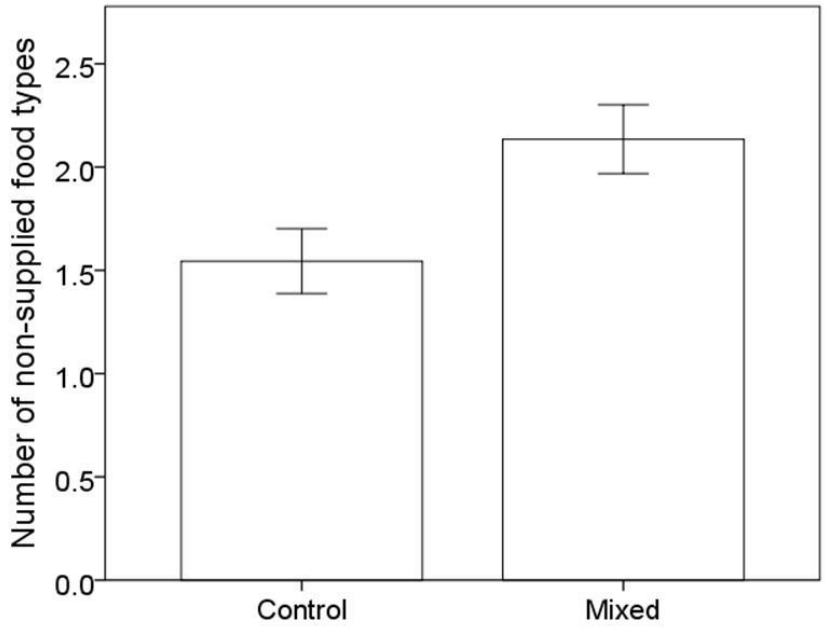


Figure 2.5. The mean number of different types of non-supplied food items identified in the crops of birds shot during the first shooting season. Error bars indicate ±1 SE.

2.3.5. Gut morphology

We extracted two principle components scores from the 11 measures of the digestive system from birds reared in 2012. Component one explained 36% of the variation and was strongly associated with intestine length, cecum 1 length and cecum 2 length. Therefore, a high PC1 score indicates an elongated hind gut. The second component explained a further 15% of the total variation with a high loading from crop height, width and depth. Therefore a high PC2 score indicates a large crop size. Birds reared on control diets had relatively longer hind guts (PC1) than those reared on

enriched diets ($F_{2,185}$ = 3.54, p = 0.031, figure 2.6). Mealworms and mixed seed birds did not differ in hind-gut length (PC1: post hoc test p = 0.30), but controls differ from birds reared with mealworms (p < 0.001) and to a lesser extent those reared with mixed seeds (p = 0.13). Sexes did not differ in their relative hind gut lengths ($F_{1,185}$ = 0.41, p = 0.52). There was no overall effect of treatment on the relative size of the crop (PC2: $F_{2,185}$ = 2.10, p = 0.13).

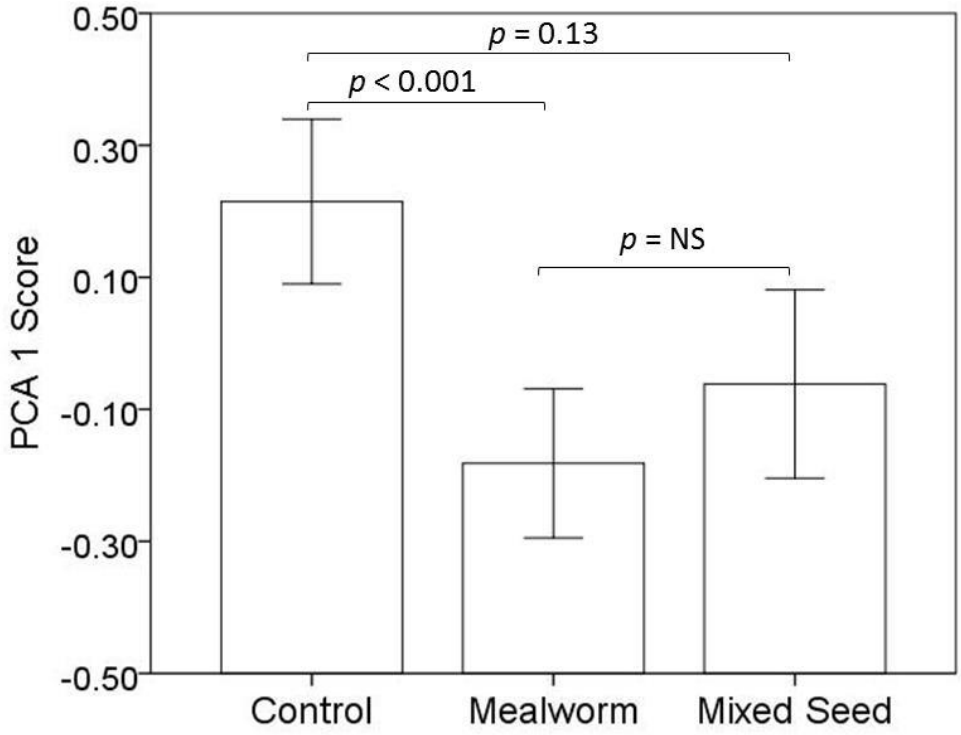


Figure 2.6. Mean PC1 score representing hind gut morphology for birds reared with either controlled or mixed diet. A low value indicates a short hind gut and high values indicates a large hind gut. Error bars indicate ±1 SE

2.4. DISCUSSION

An enriched diet early in life increased the survival of released pheasants. After a year living in the wild, we detected 2.6-5 times more birds that were reared with an enriched diet were detected compared to birds reared under control conditions. These apparently dramatic improvements in survival should be treated with some caution,

given the relatively small sample sizes that we could collect in each year. However, our replication of the finding across two separate years with distinct cohorts of released birds gives us confidence in the existence of the effect, even if not the magnitude. We do not believe that the most common sampling technique – recovery of shot birds – was biased to produce such results: we did not detect that likelihood of dispersing off the estate and so being less likely to be shot differed with rearing diet, nor did we detect mass differences across rearing treatments in the birds that were shot which may affect their flying height and hence propensity to be shot at. Instead, we believe that this increased survival may be explained by behavioural and physiological characteristics provoked by the more complex diet provided during their early rearing environment. A diverse diet, including live prey and a range of seeds and fruits, increased the handling speed of adults, resulting in more efficient foraging so that more time could be spent being vigilant. These adults also had a wider diet and were less reliant on supplemented food. This may have been facilitated by a more efficient digestive system. In both years of the study, birds reared with complex diets spent less time foraging in the wild than birds reared with the control diet, yet did not weigh any less at death, suggesting that they were more efficient in their foraging behaviour. This increased efficiency can have three positive influences on survival. First, spending less time foraging may reduce the energetic costs associated with foraging (Burrows & Hughes 1991). Second, lower foraging time reduces the time exposed to predators (Lima 1985; Guillemain *et al.* 2007). Risk of exposure to predators is particularly high for galliformes as they forage with their head and eyes directed towards the ground and therefore the probability of detecting a predator is reduced (Pulliam 1973; Fernández-Juricic *et al.* 2011). Poor anti-predator behaviour has also been observed in hand-reared whooping cranes (*Grus americana*), compared to the more naturalistic parent-reared birds (Kreger *et al.* 2005). One reason for the poor success of released grey partridge is that they do not behave adaptively in terms of vigilance and predation, determined by poor group and individual level vigilance compared to wild conspecifics (Watson, Aebischer & Cresswell 2007; Rantanen *et al.* 2010). Third, spending less time

foraging allows for the performance of other important behaviours such as being vigilant (Lima 1987). In our study, birds reared with complex diets were more vigilant than birds reared with controlled diets.

Increased foraging efficiency, exhibited by birds reared with an enriched diet, could be explained by better handling skills. Pheasants exposed to live prey from early in life were no more likely to detect novel live prey than control groups, but were about twice as fast to eat it. Insects are an important part of pheasant diet during the autumn (Lachlan & Bray 1973). Birds required the provision of a living, moving insect to learn the appropriate foraging technique. The provision of a dead insect did not improve the pheasant's ability to consume a novel insect. This also suggests that the simple nutritional benefit provided by the provision of mealworms, either alive or dead, during development did not affect the more general ability to forage more efficiently during the tests.

There was no difference between treatments in the masses of pheasants when shot, or those that we trapped. This confirms two important issues associated with manipulation in behaviour. First, the more efficient forager, in this case the birds reared with complex diets, did not simply use their new ability to eat more and increase their mass; instead they allocated the time to other behaviours including vigilance. Second, the higher vigilance adopted by birds reared with complex diets was not attributable to the starvation-predation hypothesis (Lind & Cresswell 2005; Watson, Aebischer & Cresswell 2007), as we found birds were able to forage efficiently, maintaining their vigilance levels whilst maintaining their mass gain.

Birds reared with a complex diet had greater dietary diversity after release than control birds. They were also less reliant on artificially provisioned supplementary food. Preferences for, and discrimination of, natural food sources is not innate but is shaped during early life. It is important to note that the crop samples were taken during the

shooting season when the birds still had access to supplementary feed and that across rearing treatments the mass of supplementary feed did not differ. Therefore we expected to see large quantities of keeper supplied food in the diet of all birds. The ability and propensity to utilise natural resources, even when supplementary feeding was still occurring could explain why we saw equal numbers of birds across treatments at the end of the shooting season, but why four months later we observed substantially more pheasants reared with complex diets surviving after the cessation of supplementary feeding. The ability to discriminate and choose natural food items is essential. Food discrimination may be learnt socially by local enhancement. White tailed ptarmigan (*Lagopus leucurus*) and domestic chicken (*Gallus gallus*) mothers will provide unique vocalisation to lure chicks to profitable food sources (Nicol & Pope 1996; Nicol 2004; Allen & Clarke 2005). The ability to learn foraging skills from parents was suggested to be one of the primary reasons for increased survival of parent-reared sandhill cranes (*Grus Canadensis*) compared to hand-reared individuals (Ellis *et al.* 2000). It is not just the ability to detect a variety of food items which could explain the increased foraging efficiency adopted by birds reared with the complex diets; they may have developed a wider set of handling skills necessary to obtain and ingest novel fruits and seed, essential in omnivorous pheasants. Although pheasants reared with mixed seed and fruit in 2012 did not differ from the control group in the time it took to eat a novel insect, these birds may utilise other skills that they learnt from their own rearing environment that improved their foraging efficiency upon release. Handling of food items, especially live prey, commonly improves with experience (Thornton 2008), and the development of handling techniques is essential for survival and fitness (Thornton 2008). Captive-bred black footed ferrets (*Mustela nigripes*) exposed to live prey are found to be more effective killers when adults than those fed dead prey (Miller *et al.* 1992; Vargas & Anderson 1999). Bank voles reared in captivity were unable to open nuts that were easily opened by their wild conspecifics (Mathews *et al.* 2005). Therefore, we suspect that birds reared with complex diets were both more likely to identify and sample novel food types, and be better able to process them for ingestion.

We detected morphological as well as behavioural differences according to early rearing environments. Birds reared with complex diets had shorter hind guts. This suggests that they have been consuming a high energy and low fibre diet for a period of time prior to being shot (Moss 1972; Putaala & Hissa 1995; Liukkonen-Anttila, Saartoala & Hissa 2000). Whilst we would expect gut morphologies to differ prior to release when we had control over intake, the plastic nature of the avian gastro-intestinal system suggest that these pheasants continued to find and consume a high energy and low nutrient diet after release. If the complex diet birds were restricted in their diet to the same options as those of the control birds, then we would expect that after 3-6 months in the wild the gut morphologies would converge (Redig 1989). However, birds reared with complex diets also had greater non-supplied food types, such as insects and seeds, identified in the crop analyses compared to birds reared with controlled diets, suggesting that they were utilising a higher energy and lower fibre diet to maintain the gut morphology. This is important as poor gut development is suspected to be a reason why birds do not maintain body condition after the cessation of supplementary feeding (Draycott *et al.* 1998; Draycott 2002). The increased size of the hind gut in control birds may also indirectly affect survival. Larger guts reduce an individual's ability to fly (Dudley & Vermeij 1992). Therefore a trade-off is required between maximum digestion and mobility. Here, our complex diet has not only created a gut system likely better able to cope with the more naturalistic diet that is forced on the birds after the cessation of supplementary feeding, but is also about 5% smaller, likely increasing flight efficiency and hence predator avoidance.

We conclude that in pheasants, diet, foraging behaviour, gut morphology and digestive capabilities all work together as one nutritional complex (Thomas 1987) and that a simple manipulation of diet during early development in captivity can have a cascading effect on individual survival. However, in captive rearing environments, diet is typically restricted with many intensive rearing systems using processed feed

(Liukkonen-Anttila, Putaala & Hissa 2002) which is homogenous in form and in excess (Villalba, Provenza & Manteca 2010). This food is nutritionally balanced but may not give the animal the diverse diet that it would have if it was foraging in the wild. For instance, pheasant chicks in the wild are omnivorous, feeding almost entirely on insects for the first few weeks of life and then extending their diet to include seed and plant material (Dalke 1937; Warner 1979). In captivity, pre-released chicks are fed with commercial pellet for the first 8 weeks of life (Hill & Robertson 1988j). The composition of the feed provided will mean that upon release animals will show an obvious differences in condition compared to wild animals (Putaala & Hissa 1995; Rabin 2003), being heavier and in better condition following a tailored commercial diet. However, exclusive use of artificial feed may retard the development of important foraging mechanisms. Thus releasing animals that “look” like a wild individual (Putaala & Hissa 1995; Rabin 2003), does not mean those animals have the behavioural and physiological characteristics to survive. For instance, a balanced but homogenous diet, even if nutritionally analogous to the wild, will produce an animal with a body condition comparative to its wild counterparts, but it will not have provided the necessary learning of food discrimination and handling that young in the wild experience. Pheasants are currently released in extremely high numbers to combat the poor survival after release. Therefore, rearing a bird with the ability to cope with a wild diet, leading to the subsequent improvements in survival that we detected may mean that far fewer pheasants need to be released each year whilst still maintaining economically viable levels for shooting. A reduction in the 35 million pheasants currently released in the UK would have financial, ethical and environmental benefits for both the shooting industry and natural environment as a whole (Sage, Ludolf & Robertson 2005). These results provide strong evidence for the need for careful consideration of natural rearing conditions within captive populations prior to release if we want to ensure that captive individuals have adaptive behavioural and physiological characteristics to cope with the wild stressors and survive post-release.

Chapter Three

Structural complexity in early life affects survival in released pheasants by altering roosting propensity, physiology and spatial cognitive ability

ABSTRACT

Subtle variations in early rearing environment shape and determine long lasting physiological, cognitive and behavioural processes that impact on adult fitness. We manipulated habitat complexity experienced by young pheasants (*Phasianus colchicus*) from one day old until seven weeks old, adding a third dimension in which they could interact by placing elevated perches in their rearing pens. This simple manipulation provoked an interrelated suite of physiological, cognitive and behavioural outcomes, culminating in improved survival of birds reared in more complex habitats. We identified three mechanisms to explain this. Specifically, pheasants reared with access to perches had a physiology to better enable the birds to fly to the higher branches and cope with prolonged roosting. This was accompanied by a higher propensity to roost off the ground at night. More generally, these birds had more accurate spatial memory. Consequently, birds were at a reduced risk of terrestrial predation by roosting at night, and may more quickly learn or accurately remember their new environment upon release. An individual's fitness as an adult is highly dependent on fine scale, relatively short term exposure to unpredictable conditions early in life.

3.1. INTRODUCTION

The development of an individual's physiology, behaviour, cognitive performance and neural growth can be highly plastic, shaped by conditions experienced early in life (Lindström 1999; West-Eberhard 2003; Buchanan, Grindstaff & Pravosudov 2013). Consequentially, the fitness, in terms of the survival or reproductive success of individuals is strongly influenced by early life environment either in concert with, or independent of, their genotype (Piersma & Drent 2003; Wund 2012). One facet of early life influential in development across a range of taxa is the spatial complexity of the rearing habitat. Increased habitat complexity may alter development in three, non-exclusive ways. First, a more complex environment can initiate morphological changes that mean the individual can move more effectively through such complex habitats (Robertson, Wise & Blake 1993; Ganduno-Paz, Couderc & Adams 2010; Shipov *et al.* 2010). This improved morphology may be facilitated by a reduced need to invest in features involved in defence or aggression as the value of individual dominance is reduced by the opportunities for subordinates to escape or hide (Höjesjö, Johnsson & Bohlin 2004; Tomkins *et al.* 2011). Second, a complex habitat may provide enhanced opportunities for learning which in turn affects neural development, cognitive performance and adult behaviour. Brain or brain region size is dependent on the spatial complexity of the habitat experienced during rearing (Kihslinger & Nevitt 2006; Burns, Saravanan & Helen Rodd 2009; Näslund *et al.* 2013). This may help explain differential performance in spatial cognition tasks (Wichman *et al.* 2007) or speed in finding shelters (Näslund *et al.* 2013) depending on the complexity of the rearing environment. This neural and cognitive development can be mediated by early life exposure to stress (McEwen 1999; McEwen 2008). These processes are unlikely to be independent of one another, but rather parts of a suite of coordinated changes that lead to fitness consequences; however, few studies take a holistic approach to consider the range and interplay of effects that a single early life perturbation may induce, and the resulting fitness outcomes that they impact on.

Multiple aspects of the long term morphology and behaviour of pheasants *Phasianus colchicus* are developmentally plastic, influenced by conditions experienced over short periods early in life. At the coarsest level, birds reared by hand under commercial game farming conditions tend to have lower incubation success (Sage *et al.* 2003), disperse less far and be heavier (Bagliacca *et al.* 2010) than those reared in the wild. Individuals reared by broody domestic chickens survived for longer on release into the wild than those hand-reared (Ferretti *et al.* 2012). At a finer scale, the mechanisms by which such differences may emerge can include the levels of steroid hormones in the egg which can affect wattle colour and other male sexual traits, digit ratio, patterns of female mate choice and male sexual behaviour (Romano *et al.* 2005; Rubolini *et al.* 2006; Rubolini *et al.* 2007; Saino *et al.* 2007; Bonisoli-Alquati *et al.* 2011a; Bonisoli-Alquati *et al.* 2011c; Rubolini *et al.* 2014). The diet that a bird experiences in its first few weeks of life affects its tarsal size and symmetry (Ohlsson & Smith 2001), male sexual ornaments (Ohlsson *et al.* 2002), body condition (Sage, Putaala & Woodburn 2002), body size (Orledge *et al.* 2012a), and parasite load (Orledge *et al.* 2012b). Such developmental plasticity is likely to have fitness consequences for pheasants, and indeed other animals, artificially reared and released. Pheasants offer a further advantage for studies of developmental plasticity: they can be reared artificially, in large numbers, under tightly controlled experimental conditions free from parental influence, yet be released into the wild where they are exposed to natural selective pressures providing meaningful measures of fitness.

Captive rearing typically takes place in unnatural and often spatially simple habitats (Hill & Robertson 1988j; Buner & Schaub 2008). We concentrated on the structural enrichment that chicks experienced early in life, and asked how provision of perches may provoke complex and long lasting behavioural, physiological and cognitive developments that impact the fate of released birds. The highest loss of reared birds is observed in the first weeks after release into the wild and the main

cause of mortality is predation (Hessler *et al.* 1970; Krauss, Graves & Zervanos 1987; Parish & Sotherton 2007). Inadequate anti-predator behaviours have been linked to the observed high mortality (Wallace 1994; van Heezik, Seddon & Maloney 1999; Fischer & Lindenmayer 2000). Birds naturally use perches as a form of anti-predation behaviour (Wood-Gush & Duncan 1976; Newberry, Estevez & Keeling 2001). An absence of perching opportunities during captive rearing may inhibit individual opportunities for learning of this essential behaviour. Poor roosting behaviour has fitness consequences: high mortality in released cheer pheasants (*Catreus wallichi*) (Garson, Young & Kaul 1992) and grey partridge (*Perdix perdix*) (Dowell 1990) have been attributed to poor roosting behaviour. Two mechanisms may influence chances of survival upon release; 1) specifically, the development of a functional antipredator behaviour, in this case roosting including the propensity to roost on elevated branches at night and the physiological characteristics required for this; and 2) more generally, the cognitive and social influences driven by a more naturalistic environment affecting cognitive ability which have fitness benefits beyond simple roosting behaviour. Therefore, we predict that individuals reared in a spatially complex environment with access to perches will survive better as adults when released into the wild.

Access to perches in captive reared birds (chickens, *Gallus gallus domesticus*) affects readiness to perch as an adult (Gunnarsson 1999; Gunnarsson *et al.* 2000) and crucially, propensity to perch at night (Olsson & Keeling 2000). Exposure to perches influences the development of the leg bones (greater bone mass (Shipov *et al.* 2010) and bone volume (Hughes *et al.* 1993)) that help the bird to perch, and flight muscle required to reach the perches (Robertson, Wise & Blake 1993). Poor development of flight muscles due to lack of perches may explain the poorer flying ability of captive-reared birds compared to wild ones in terms of shorter flight distances (Perez, Wilson & Gruen 2002; Hess *et al.* 2005), endurance (Putaala *et al.* 1997) and take off ability (Putaala & Hissa 1995). Therefore, we predict that early access to perches will: 1) increase the readiness of a bird to perch upon first release; and 2) develop the

physiological characteristics that will aid the bird to access and remain on the perch for an extensive period of time.

Early exposure to a spatially complex rearing environment in which a third dimension is added through the provision of perches is also likely to have a suite of broader effects. Chickens with access to perches are better at using three dimensional space (Wichman *et al.* 2007), and rearing without perches can impair spatial cognitive tasks, such as navigating the environment (Gunnarsson *et al.* 2000). We predict that the provision of perches during development will improve spatial ability in cognitive tasks.

3.2. METHODS

3.2.1. Rearing and release into the wild

We reared and released pheasant chicks in 2013 on the Middleton Estate, Hampshire. The estate hosts a game shoot from October until February and employs gamekeepers to manage the release of pheasants through habitat management, providing supplementary food, and controlling predator numbers. In May 2013 we purchased 900 one day old pheasant chicks from a commercial supplier. Chicks were marked using individual numbered plastic patagial wing tags (Roxan Ltd) and randomly allocated to three treatment groups, differing in their access to perching. In treatment 1, a control, chicks were reared under standard commercial rearing conditions with no access to perches. In treatment 2, natural perches, chicks were reared under the same standard rearing conditions as the control treatment, but with access to natural perches, in the form of hazel (*Corylus avellana*) boughs. In treatment 3, artificial perches, chicks were reared under standard rearing conditions with access to artificial perches, in the form of plastic conduit piping.

We established ten replicates of each treatment, with each replicate containing 30 chicks. Each replicate was housed separately in a heated shed (1.3m x 1.3m) for the first two weeks of life. For the next five weeks they had access to an open grass run (1.3m x 6.8m), as well as the shed. Current minimum welfare recommendations for intensively reared adult chickens suggests a perching distance of 0.15m per bird (CEC 1999; Appleby 2003); adhering to this figure we would need a minimum of 4.5m of perches, therefore, to ensure that all birds had sufficient access to perches we provided a total of 6.4 meters of perches. In the wild a pheasant chick will encounter perches of differing sizes, to best replicate this we provided perches which ranged in diameter. For treatments 2 and 3, we constructed three perches inside the shed and a further three perches in the open grass run; for diameters, length and height from the ground of the perches see Table 3.1. Water and age appropriate commercial game feed was available *ad lib* throughout the rearing period. To maintain stocking density, any bird that died during the rearing period was replaced by a sex-matched individual. Replacement chicks were excluded from subsequent analyses. A preliminary analysis of the data revealed no qualitative difference between the artificial and natural perching groups. Therefore, we combined birds from the two treatments for the remainder of our analyses and simply compared those with perches to those without. The birds were simultaneously being subjected to a dietary manipulation in a fully balanced 3x2 design, where birds were either fed a control or an enriched diet (mixed bird seed and live mealworms see chapter 2).Our preliminary analyses revealed no qualitative effects of diet on the measures of interest here, so we either combined birds from both diets for non-parametric analyses, or included diet as a factor in our models.

At seven weeks old, the birds from all treatments were mixed together and placed into one of two release pens on the estate. The pens measured on average 12249 m^2. Release pens typically consist of a wire mesh fence around a 2m high enclosure of woodland into which many hundreds, occasionally several thousands, of pheasants are released (GWCT 1991). The size of pens required in this system

depends on the scale of the release and adherence to good practice. The Game and Wildlife Conservation Trust recommends 1000 birds per hectare pen (Sage & Swan 2003). The primary function of the pen is to protect the young captive-reared pheasants from terrestrial predators. All pens were unroofed, so that birds could disperse at will from the pen and were exposed to the threat of avian predation. The pens contained water and food ad lib.

Table 3.1. Representing the dimensions and the height of perches used in both the house and the outside run.

Location	Diameter (mm)	Length (m)	Height from floor (m)
House	20	0.8	0.15
	25	0.8	0.3
	35	1.2	1
Run	20	1.2	1.2
	25	1.2	0.8
	35	1.2	0.5

3.2.2. Measuring survival in the wild

Survival in the wild was measured using three methods. Prior to the start of the breeding season in April 2014, birds that died of natural causes were collected by searching the estate and surrounding areas. Post release and prior to the hunting season (June 2013-October 2013) we conducted daily searches of areas of the estate. During the hunting season (October 2013-February 2014) the area was visited less frequently but more methodically as beaters, engaged in driving the game towards the

waiting guns, were informed of the project and searched for carcases and tags as they walked through the estate. After the shooting season (March 2014-June 2014) the same area was visited about once a week. We conducted more detailed evaluation of mortality of a subset of birds which survived the winter and shooting season. In February and March 2014 following the shooting season, we captured birds using funnel traps baited with grain (Taber & Cowan 1969). Males and females from known rearing conditions were fitted with necklace radio-transmitters then radio tracked using a portable receiver (e.g. Sage *et al.* 2003) Radio transmitters were 13 grams, around 1.5% or less of body weight. We followed the fates of these birds over the following four months, radio-tracking birds around twice a week, access permitting. For both the initially released and radio-tagged birds, we picked up carcasses of the pheasants that we found and identified them by their numbered wing tag. Some dead birds were damaged, indicating that they had been predated. If there was no external damage to the bird, we suspect that it died of other causes, perhaps disease. However, it is possible that birds we recovered with marks of predation had actually died of other causes and their body had been scavenged. Therefore we could not confidently discriminate natural causes of death so we combined them in to a single category of natural deaths. Finally the number of birds that were shot during the second hunting season (October 2014 – February 2015) was recorded; this indicated the number of birds that survived 18 months including a breeding season.

We tested whether the number of birds dying in the first year after release differed between treatments. For the analysis of pre-March 2014 deaths, we tested whether the numbers of dead birds that we observed differed from those expected given a release ratio of two birds reared with perches to each one control bird. For analysis of March 2014 – August 2014 deaths, we suspected that the expected ratios of treatment to control birds had changed, but we could not determine accurately what they were. Therefore, we simply compared the ratio of dead to living individuals from the sample of birds that we had radio-tagged and tracked. For the analysis of the birds

that survived 18 months in the wild, we again expected that ratios of treatment to control had changed, but we could not determine accurately what they were. Therefore we used a chi-square test to ask whether rearing treatment affected the number of birds surviving 18 months in the wild and then shot.

3.2.3. Measuring perching behaviour in the wild

For the first two weeks after release into the wild we determined how many birds from each treatment could be seen perching. Between the 45 minutes before and 60 minutes after last light we observed birds in the release pens, using a IR illuminated night-vision monocular where necessary, to record which birds were roosting on perches off the ground. We tested whether the number of birds from each rearing condition seen perching differed from the ratios of birds from each condition that had been released into the pens. We repeated these comparisons after the birds had lived for 6 weeks in the wild to determine if there was a long-term effect of early access to perches on an individual's propensity to perch.

3.2.4. Measuring morphological effects of early access to perches

We recorded the mass (Slater Super Samson spring balance – precision 5g) and tarsus thickness (callipers – precision 0.1mm) of all birds (n = 900) upon release into the wild at seven weeks old. A general linear mixed model (GLMM) was used to ask if morphometrics differed with early access to perching, considering sex differences, with the house as a random factor.

3.2.5. Measuring prolonged morphological effects of early access to perches

To determine if there was a long term effect of rearing treatment on morphology we collected all shot birds (n=202) and weighed them and measured tarsus thickness within four hours of death. We also removed left tibias from 40 birds shot during the shooting season. They were striped of soft tissue by hand and the bone cap removed. The bone length was measured using a calliper and bones were weighed on a

precision balance. A midline was marked and the maximum and minimum outer diameter (diaphysis diameter) was measured. Using a saw we cut through the midline and measured the maximum and minimum medullary canal diameter. Three indices were then calculated based on the following formulae: 1) tibiotarsal index = [(Diaphysis diameter-medullary canal diameter)/diaphysis diameter]*100 (Barnett & Nordin 1960); 2) robusticity index: bone length/cube root of bone weight (Riesenfeld 1972); 3) bone weight length index: bone weight/length (Seedor, Quartuccio & Thompson 1991). A GLM was used to ask if there early access to perching affected the different morphometrics, whilst considering sex differences.

3.2.6. Measuring spatial memory: eight arm radial maze test

We presented 27 six week old chicks, randomly chosen from each treatment with an eight arm radial arm maze (Figure 3.1), testing spatial working memory. The cognitive testing facility was located on the same field as the rearing facility and for the duration of the habituation and testing the birds were housed separate from the main group but under the same environmental conditions, except for reduced density. In the centre of the radial arm maze was a circular starting arena and at the end of each arm, behind a barrier was a single mealworm. The chicks became accustomed to the arena for 20 minutes a day, twice a day for four days. On days one and two, the birds were exposed to the radial maze in groups of three individuals with rewarded food (chick crumb and dead mealworms). Day three, the birds were exposed to the radial maze singly with rewarded food. Day four, the birds were exposed to the radial maze singly with the rewarded food placed only behind the goal. Testing started after the fourth day of training. To solve the test correctly a bird entered each arm once and ate the mealworm in the bowl. If a bird re-entered an arm that had already had the mealworm eaten it was recorded as an error, re-entry was considered as a bird entering an arm a distance of one half of its body length. The barrier meant that the bird had to be near the bottom of the arm to see the mealworm; therefore erroneous movements were easily determined. We recorded the latency and the number of errors made for each

correct arm entered. The test was stopped after 15 minutes if not completed. The walls of the arena were 55 cm high and wire mesh was used as the roof. This enabled birds to look up to orientate. To help the birds orientate we provided a large red feature (47kg gas bottle) and the walls of the test room were different colours. The testing took place over 3 days between 7:30h and 10:00h and 18:30h and 20:00h, to best replicate foraging time in the wild, also to reduce the stress of moving and testing birds during the midday sun. We used a GLM to ask if the errors made during the first eight choices differed with early access to perching.

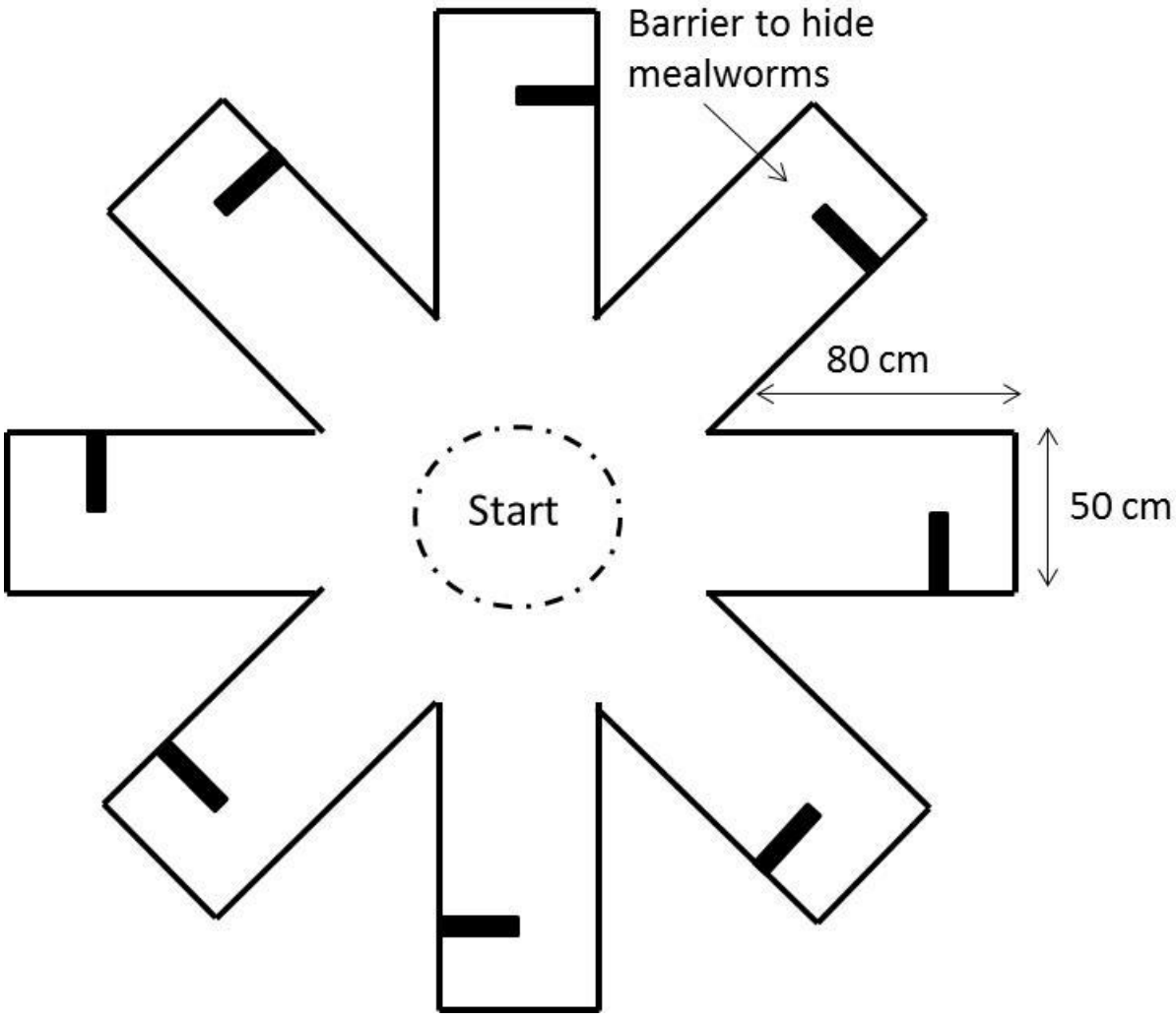


Figure 3.1. The eight arm radial maze: Height of the maze was 55cm. The entire roof of the maze was constructed out of wire mesh to allow birds to orientate using visual landmarks in the room. The barrier hiding the mealworms was 25cm wide.

3.2.7. Ethical note

All birds were reared using commercial procedures that adhere to the DEFRA Code of Practice for the Welfare of Gamebirds Reared for Sporting Purposes (DEFRA 2009). For behavioural testing, birds were subjected to minimal handling, a bird was only asked to perform one test. Released birds were attended by a game keeper. Once birds were dispersed from the release pen, the keepers supplied supplementary feed and water. The birds were shot as part of a commercial shoot, and were not specifically shot for this study. The work was approved by the University of Exeter Psychology Ethics Committee and conducted under Home Office licence number PPL30/2942.

3.3. RESULTS

3.3.1. Survival

Birds reared with perches survived better immediately post-release and through their first winter. Fourteen birds that had been reared under the control conditions were detected as having died of natural causes after release prior to the start of the breeding season compared with only four that had been reared with perches (χ^2= 16.00, p < 0.001). The rearing treatment did not affect the number of birds that were shot (χ^2= 0.93, p = 0.33) or the number of birds dispersing from the estate (χ^2 = 1.50, p = 0.22) prior to February.

This effect of early rearing environment was lost once the shooting season ended and the breeding season began. Of the 18 birds reared with perches who we radio-tagged in March, 13 died of natural causes by the end of the breeding season in July, compared with three of the eight birds that had been reared without perches (χ^2_c = 1.55, p = 0.21). There was also no difference in number of birds shot in the second shooting season (winter 2014/2015) when the birds were over 18 months old (χ^2 = 1.00, p = 0.32).

3.3.2. Perching behaviour in the wild

More birds reared with access to perches were observed roosting at elevation at night in the wild during the first two weeks after release than birds reared with control conditions (χ^2 = 15.82, p < 0.001, Figure 3.2). This difference across the treatments disappeared after 6-7 weeks, with no more perch-reared birds roosting at elevation than control birds (χ^2 = 0.53, p = 0.47, figure 3.3).

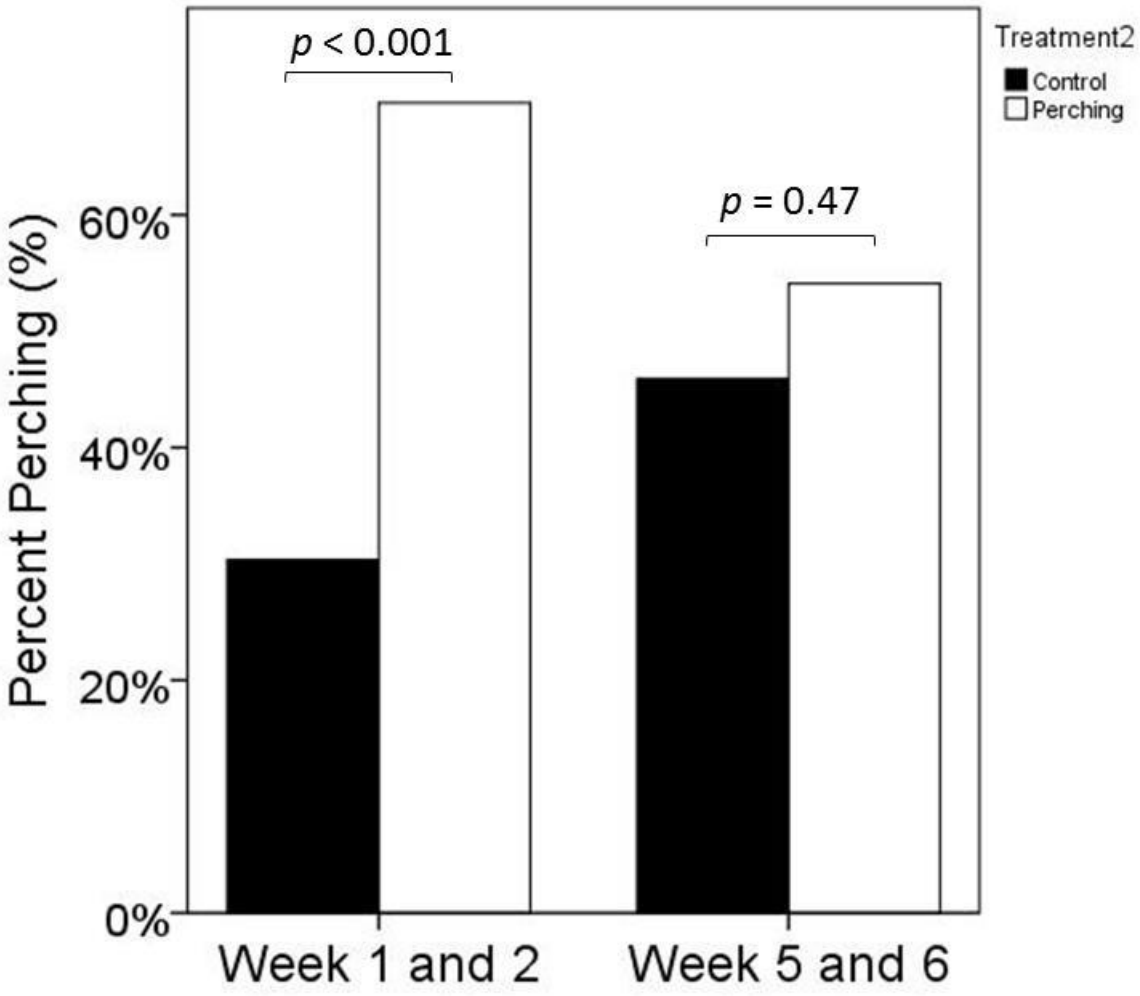


Figure 3.2. The percentage of birds observed perching from different rearing treatments for the first two weeks after release and weeks five and six after release.

3.3.3. *Body mass*

Early access to perches affected the mass of a bird at the time of their release (GLMM: Treatment: $F_{1,874}$ = 13.79, p < 0.001), which was primarily driven by mass

differences in males, with males reared with access to perches being heavier than males reared without access to perches (post hoc test $p < 0.001$) (GLMM: Treatment*Sex: $F_{1,874} = 7.59$, $p = 0.006$, figure 3.3). As expected, males were heavier than females (GLMM: Sex: $F_{1,874} = 527.36$, $p < 0.001$). There was no prolonged effect of early access to perches on the mass of birds recorded when they were shot several months after release (GLM: Treatment: $F_{1,118} = 0.97$, $p = 0.33$), and males did not show the same difference in mass between treatment groups as previously shown at release (GLM: Treatment*Sex: $F_{1,118} = 0.37$, $p = 0.55$).

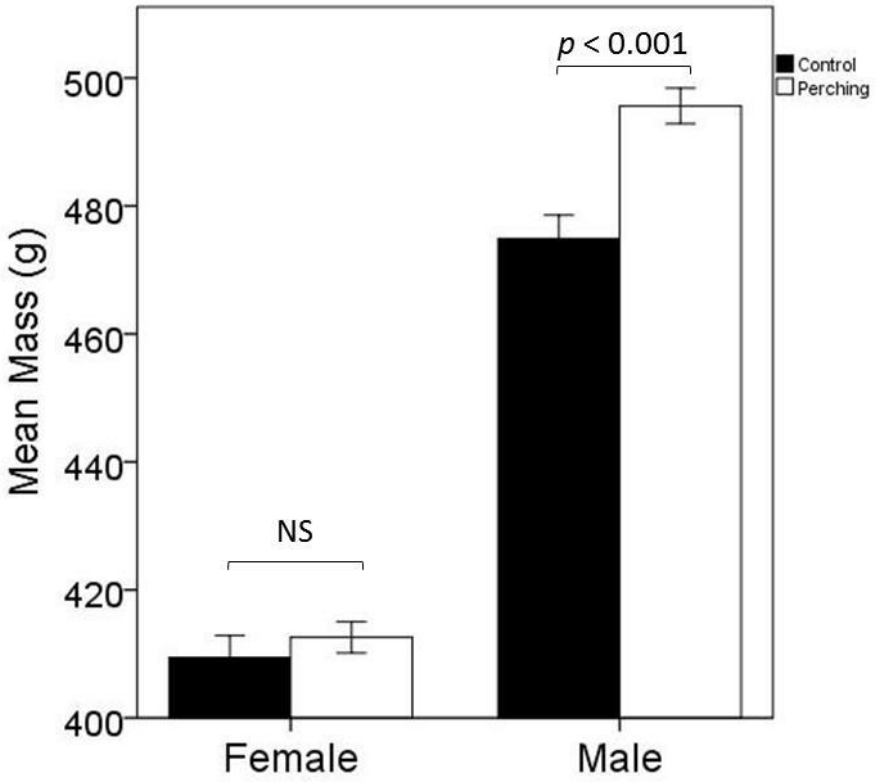


Figure 3.3. The mean mass of birds upon release into the wild for each males and females clustered by rearing treatment. Error bars indicate ± 1SE

3.3.4. Tarsus thickness

Early access to perches affected the tarsus thickness of birds at the time of release (GLMM: Treatment: $F_{1,879} = 8.83$, $p < 0.001$), which was primarily driven by tarsus thickness differences in males (post hoc test $p < 0.001$) (GLMM: Treatment*Sex:

$F_{1,879}$ = 4.15, p = 0.042, Figure 3.4). As expected, males has thicker tarsus than females (GLMM: Sex $_{1,879}$ = 530.70, p < 0.001).

This difference was lost when we measured the tarsi of birds that had been shot four to eight months later (GLM: Treatment: $F_{1,163}$ = 0.67, p = 0.42). There was also no difference in bone mineralisation in these shot birds (Tibiotarsal index GLM: Treatment: $F_{1,29}$ = 2.49, p = 0.13; robusticity index GLM: Treatment: $F_{1,29}$ = 2.03, p = 0.17; bone weight/length index GLM: Treatment: $F_{1,29}$ = 2.54, p = 0.12).

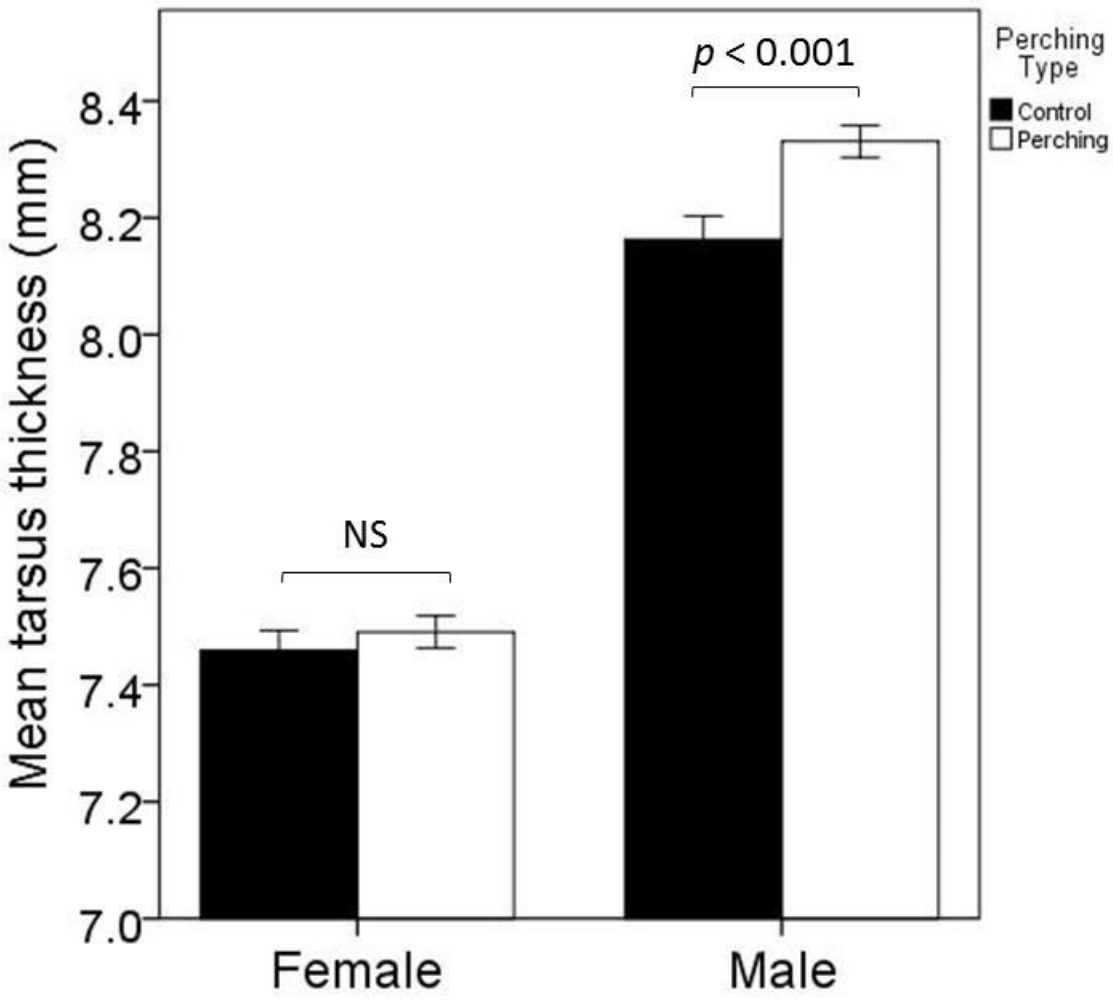


Figure 3.4. The mean tarsus thickness of males and females upon release reared with either access to perches (perching) or birds reared without access to perches (control). Error bars indicate ± 1SE.

3.3.5. Cognitive performance in a spatial ability task

Birds reared without access to perches made more errors in their first eight choices in the radial arm maze than birds reared with access to perching (GLM: Treatment: $F_{1,23} = 15.59$, $p = 0.015$, figure 3.5). The effect of treatment was not affected by the sex of the bird (GLM: Treatment*Sex: $F_{1,23} = 0.99$, $p = 0.51$). Only 6 birds completed the trial (Perches = 5; Control = 1). The rearing treatment ($F_{1,22} = 0.12$, $p = 0.73$) or sex ($F_{1,22} = 0.24$, $p = 0.63$) did not affect the time a bird took to enter four successful radial arms.

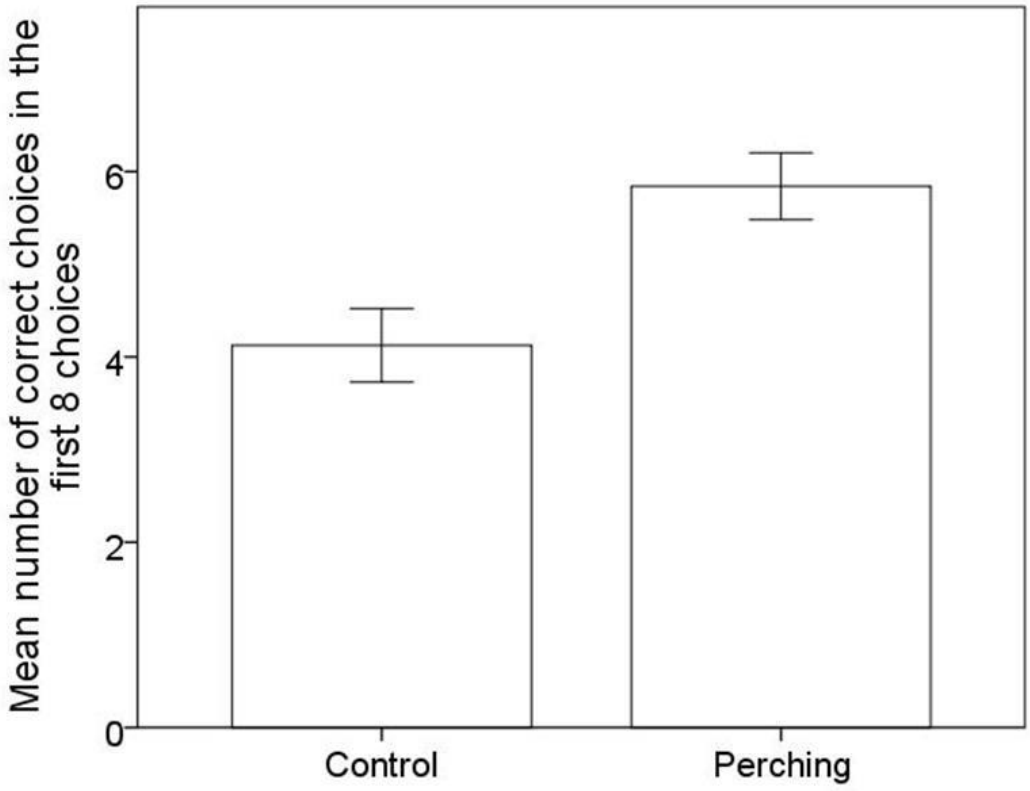


Figure 3.5. The mean number of correct choices made for the first eight choices when presented with an eight arm radial maze for birds reared with or without access to perches. Error bars indicate ± 1SE.

3.4. DISCUSSION

Pheasants exhibit a broad suite of coordinated developmental changes, driven by a simple alteration in the spatial complexity of their rearing environment early in their life where the addition of perches opens up a third dimension for them to explore and utilise. Natural variation in exposure to perching sites may be due to local microhabitat features, or the length of time that the precocial pheasant chick spends with its parent who demonstrates perch use (Collias & Joos 1953). This exposure to perching influences their morphology, behaviour, cognitive performance and ultimately their survival. Birds reared in the more spatially complex habitat were heavier, had thicker tarsi, were more likely to utilise elevated perch sites in the wild, and exhibited more accurate memory of locations in a radial maze task during and immediately after the experimental rearing conditions had been imposed. These effects arise through the plastic development of skeletal, muscular and neural features. Some of these effects, specifically those directly associated with increased propensity to use perches to roost off the ground at night (mass, tarsus thickness and nocturnal perching) are lost fairly rapidly once the environmental conditions are equalised. However, for released pheasants (Brittas *et al.* 1992), and indeed many young birds (e.g. Ghalambor & Martin 2001) the period critical to their survival is in the first few weeks of life and such plasticity has fitness consequences manifested at a young age. These changes occurring early in life may explain the increased likelihood of post-release survival, at least in the first few months of life, of birds that had been reared in the spatially more complex habitat in the face of natural selective forces. Other effects which have a less direct link to perching such as the development of better spatial memory may persist for a least several months. Unfortunately we did not observe the numbers and identities of birds using perches whilst in the rearing pens. This would have allowed us to make better correlations between individuals and their corresponding development and survival rather than simply focussing at the population level.

Improved survival corresponding to early rearing environment was observed over the first eight months post-release. This was dramatic, with over three times more birds raised in control conditions being found dead when compared to those reared with perches. We suspect that improved survival on initial release was due to the propensity for a bird that had been reared with perches to roost off the ground at night. A similar mechanism was observed in captive galliformes, where chickens reared with perches in captivity were shown to perch more readily as adults (Gunnarsson 1999; Gunnarsson *et al.* 2000), in particular at night (Olsson & Keeling 2000). Roosting at night is an essential anti-predation behaviour for ground dwelling birds (Wood-Gush & Duncan 1976), especially where the crepuscular and terrestrial fox is the biggest cause of predation (Brittas *et al.* 1992; Parish & Sotherton 2007). This may explain the extremely high mortality experienced by released pheasants reared in conventional, unenriched habitats: Within a few months of release 25% of birds die, with 75% of these being predated (Turner 2004). Robertson (1988) reported up to 70% of all known bird deaths were attributed to predation within the first year of release. In a more extreme case Hessler *et al.* (1970) observed 81% losses of birds released into the wild within the first month with up to 90% of these losses attributed to predation. Burger (1964) reported 65% losses in the first week alone. Such a winnowing process early in life may rapidly remove the variance on which selection can act later on in life.

Differential survival between rearing treatments was not detected after six months. This may be because a large proportion of poorly developed birds were removed from the population in the initial six months, meaning that comparisons later in the year were between biased samples including disproportionate numbers of birds from simple rearing habitats that were better survivors for reasons other than their roosting behaviour. Alternatively, survivors from the spatially poor rearing environment may compensate for their early-life deficiencies in habitat complexity through exposure to complex environments post-release. Prior to release the mass and tarsal thickness was greater in seven-week old birds reared with access to perches compared to control

birds, but these effects were lost over subsequent months, such that no differences were observed in birds that had been shot. The initial enhancement of mass is likely explained by the spatial complexity of their rearing environment, because our experimental and analytical design controlled for alternative explanations such as diet. Barren environments are believed to restrict the development of flight muscles by removing an incentive to engage in controlled flight to access the perches (Robertson, Wise & Blake 1993). In addition, small diameter perches induce birds to wing-flap to balance (Pickel, Scholz & Schrader 2010). Both these features will help develop the associated muscles and could explain the differences in mass upon release. We do not know why mass gain was greater in males than females. Increased pectoral muscle mass increases take off power which benefits predator evasion (Tobalske & Dial 2000), and could enable the birds to reach the higher and safer perches post-release. A second morphological enlargement, increased tarsus thickness, can also be explained by the complexity of the environment. For chickens reared in captivity with access to perches bone calcification resulted in tarsi becoming larger and stronger (Hughes *et al.* 1993; Fleming *et al.* 1994; Shipov *et al.* 2010). The combination of bone strength and muscle strength suggests that upon release, and after release, the birds had the physiology to cope with prolonged roosting. However, birds reared in control environments which survived the first three months of release developed mass and tarsi equal to those of birds reared with perches. This convergence may be because within six weeks of release into the wild there was no difference in the number of birds roosting from either rearing treatment. This suggests that birds reared with the controlled treatment learned from their conspecifics. In the wild, offspring learn elevated roosting from their mothers who promote climbing and flying up to roost with the use of calls (Collias & Joos 1953) .

A potentially longer lasting effect of the early rearing environment may be seen as a consequence of the differences observed in the tests of spatial working memory. Birds reared with perches made significantly fewer errors when placed in a radial arm

maze than control birds. The radial arm maze is used extensively to measure spatial ability (Lipp *et al.* 2001; Wichman *et al.* 2007) and our results indicate that birds reared with early access to perches have a higher level of spatial ability. An increase in spatial ability was also observed in chickens reared with access to perches (Gunnarsson *et al.* 2000; Wichman *et al.* 2007). An enhanced spatial ability may be facilitated by differential hippocampus development (Sherry, Jacobs & Gaulin 1992; Bird & Burgess 2008). Comparisons across species reveal that this effect may be adaptive; habitat complexity is positively correlated with brain (region) size in chipmunks (Budeau & Verts 1986), bats (Safi & Dechmann 2005), ungulates (Shultz & Dunbar 2006) and cichlids (Pollen *et al.* 2007) and salmonids (Kihslinger & Nevitt 2006). Differing access to perches during development may bring additional fitness benefits beyond simply a propensity to perch. It may permit better memory of food or shelter sites (Basil *et al.* 1996), more direct movement between sites (Gagliardo, Ioalé & Bingman 1999) or increased object exploration (Mettke-Hofmann 2007). Such effects may persist even when the initial trigger for differential development, that is access to perches, has been removed.

Developmental plasticity can be harnessed by game managers and reintroduction biologists. The release of birds that “look” like a wild individual (Putaala & Hissa 1995; Rabin 2003) does not mean that these animals have the behavioural, physiological and cognitive characteristics to survive. A well-managed, barren rearing environment may mass-produce birds which are healthy and in similar condition to their wild conspecifics on release, but a lack of early life experiences and opportunities can prove detrimental to their survival on release. We found over three times more dead birds from the control environment than from groups reared with perches. Releasing birds with the behavioural, cognitive and physiological developments to survive will mean that fewer bird are required to be released each year and still maintain the same shooting bag that is essential for the economic success of the industry. A reduction in the ~35million pheasants released each year (PACEC 2008) would deliver obvious

ethical advantages, as well as economic and ecological advantages. Releasing fewer birds at lower densities would reduce disease burdens (Gortázar *et al.* 2006) or enhance biodiversity or survival of key indicator species (Sage, Ludolf & Robertson 2005; Draycott, Hoodless & Sage 2008a; Sage *et al.* 2009; Callegari *et al.* 2014).

Our manipulation of a single aspect of early life environment, namely habitat complexity, clearly illustrates the broad range of proximate and ultimate consequences arising from this simple change. Many studies of developmental plasticity concentrate on single effects, or a small number of tightly inter-related effects. We suggest that such effects are unlikely to occur in isolation, but instead comprise part of a larger correlated suite of changes, which may have unexpected consequences. For example, alteration of spatial performance may exclusively facilitate better use of perches, but it may additionally affect foraging success or home range use. All these alterations are likely to influence fitness outcomes, and hence the way that selection acts on plasticity. Furthermore, the need to tightly control early life conditions in studies mean that manipulations are typically carried out in captive conditions; coupled with the difficulty of releasing lab-reared organisms, especially vertebrates, into the wild, assessing the consequences of the manipulation under natural conditions is difficult or impossible. Therefore, our understanding of the evolutionary basis of developmental plasticity is likely to be incomplete unless we consider both the diverse range of effects which changes in any one early life factor initiates, and the fitness consequences for an individual in its natural environment.

Chapter Four

A successful reintroduction programme: the importance of pre-release welfare

ABSTRACT

Conditions experienced during early development can influence an individual's behavioural, physiological and cognitive developments. Reintroduction biologists utilise this developmental plasticity to try and mitigate developmental deficiencies associated with translocated animals that often lead to high mortality and poor reproductive success. However efforts to promote the development of survival skills in captivity, through the application of a more naturalistic environment, can compromise welfare. Therefore there is a tension. Extremely high welfare standards can be implemented which maximise fitness and produce large numbers of "healthy animals" at the point of release who have been protected and cosseted through rearing, and as such may be poorly adapted to conditions in the wild, post release. Alternatively, animals may be exposed to more difficult, but controlled, conditions during rearing which may expose them to limited pain, suffering or distress for short periods, but also prepare them for survival post post-release. This dilemma exists for both animals reared and released for conservation and animals released for sporting purposes.

The pheasant provides an ideal system. Released pheasants suffer from high mortality and poor reproductive success. There is a concerted effort to improve post release survival through the manipulation of rearing environments, however, with 35 million birds released in the UK each year; there is also a moral imperative that these conditions do not compromise welfare. The pheasant system allows for high sample sizes, replicated conditions and incorporation of welfare assays from the captive galliform industry.

We explored whether welfare assays, such as aggression, time spent conducting comfort behaviours, mortality and stereotypical displacement preening behaviours differed between environments that has the primary aim of

improving developments suited for wild living, in the form of increased dietary breadth and increased habitat complexity, compared to control systems that simply replicate the barren rearing regime.

In both manipulations we observed no negative effects on welfare. Instead we saw improvements to important components of welfare. Birds reared with a diet that replicated the diet of age-specific wild conspecifics spent more time conducting comfort behaviours. Birds reared with access to perches were subjected to less aggression, perhaps because access to perches reduced ground level stocking density and provided access to refuges.

Our manipulations during early rearing, with the primary aim of improving post-release survival of the birds, improved important components of welfare; demonstrating that preparing birds for release need not compromise their welfare. We highlight the trade-off between pre-release welfare, development and post-release success. We emphasise the need to not simply look at the post release outcomes of a translocation programme and hope that others take our lead and include the pre-release welfare in studies on reintroduction.

4.1. INTRODUCTION

Captive reared animals released as part of conservation programme often suffer from high mortality and poor reproductive success (Kleiman 1989; Snyder *et al.* 1996). This has been attributed to developmental deficiencies which make released animals unable to compete with wild conspecifics (Fleming & Gross 1993), unable to appropriately detect and assimilate food items (Putaala & Hissa 1995; Ellis *et al.* 2000; Jule, Leaver & Lea 2008) or avoid predators (Griffin, Blumstein & Evans 2000). It is well established that conditions experienced during early rearing can have an effect on morphological, behavioural and cognitive developments (Lindström 1999; West-Eberhard 2003; Buchanan, Grindstaff & Pravosudov 2013) and reintroduction biologists utilise this developmental plasticity by manipulating a captive environment to promote developments in an effort to mitigate the deficiencies associated with released animals (van Heezik, Seddon & Maloney 1999; Vickery & Mason 2003). One of the best ways to promote naturalistic survival skills is to create a captive environment that better replicates conditions an individual would experience in the wild (Shepherdson 1994). However, wild animals are subjected to fear, stress and discomfort, all features that would compromise welfare, but captive managers are responsible for welfare and the production of healthy animals during the time the animal is in captivity (Carlstead & Shepherdson 1994; Swaisgood 2007). Therefore, rearing animals for release poses a dilemma; do you cosset the captive stock entirely, actively follow the five freedoms (FAWC 1993) and consider the duration, frequency intensity and valence of any potential manipulation (Russell & Barrett 1999; Mendl, Burman & Paul 2010), maximising the welfare of the individual during its time in captivity, but in so doing release individuals which are poorly prepared for life in the wild. Or, do you expose individuals to dangers, stress and discomfort early in life to better prepare it for survival after release into the wild? The balance between short term maximum welfare and long term exposure to danger and discomfort needs to be determined and future work could concentrate on this.

This dilemma in not restricted to animals released for conservation purposes, but also exists in animals that are released for sport. 5 x 10^9 salmon (*Salmo salar*) are released each year around the world, with around a 5% survival to adulthood (McNeil 1991). 40 million game birds are released in the UK as a part of annual restocking events (PACEC 2008), with similar poor success (Brittas *et al.* 1992; Buner, Browne & Aebischer 2011). These animals are reared as part of a business, and therefore subject to additional trade-offs between pre-release welfare, post release survival, numbers for release and financial costs associated with rearing. A reluctance to mend something which is apparently not broken (i.e. they adhere to the codes of practice (DEFRA 2009)), the financial costs associated with applying these manipulations, combined with the fear that manipulations may compromise welfare, may mean that environmental manipulations to promote the development of important survival traits are not even attempted.

There is little research conducted in either context. One of the reasons is that welfare is not studied in animals reared for release because wildlife managers often lack the tools and the knowledge to assay behaviour indicators (Teixeira *et al.* 2007). Also, many translocation programmes using captive propagation involve endangered animals; therefore there are often low sample sizes, lack of replicated conditions and a reluctance to manipulate the environment through fear of detriments to welfare and development (Seddon, Armstrong & Maloney 2007; Armstrong & Seddon 2008). The pheasant offers a great model system for understanding the effects of captive rearing for both conservation and sporting reasons. The pheasant is released in high numbers for sporting purposes but can act as a surrogate species for many galliformes including the red-listed (malleefowl *Leipoa ocellata* (Priddel & Wheeler 1999), greater-sage grouse *Centrocercus urophasianus* (Musil, Reese & Connelly 1994; Reese & Connelly 1997), sharp-tailed grouse *Tympanuchus phaianellus* (Rodgers 1992), white tailed ptarmigan *Lagopus leucurus* (Starling 1991), and the grey partridge (Buner & Schaub

2008; Buner, Browne & Aebischer 2011). Although little research on pheasant welfare has been conducted, there are well established assays of galliform welfare thanks to work on captive chickens.

The current pheasant rearing regime uses a relatively barren and parasite free environment, adlib food provision, the use of mechanical “bits” to reduce the effects of aggression, permanent warmth and shelter, medication from disease, and fences to exclude predators. This process allows for game-rearers to produce high numbers of “healthy birds” whilst adhering to DEFRA codes of practice (DEFRA 2009). However, pheasants upon release suffer from high mortality (Turner 2004), with released birds being more vulnerable to mortality than wild birds (Hessler *et al.* 1970; Sage & Robertson 2000), attributed to inadequate anti- predation behaviours (Garson, Young & Kaul 1992) and poor foraging technique (Brittas *et al.* 1992; Robertson 1997; Sage & Robertson 2000). Released pheasants have lower reproductive success than wild birds. Released males are unable to compete with wild conspecifics (Anderson 1964) and have smaller harem sizes (Hill & Robertson 1988a). Released females have lower incubation success (Sage *et al.* 2003) and brooding success (Hill & Robertson 1988a) compared to wild birds. Such developmental deficiencies are attributed to a rearing environment which does not allow for the appropriate behavioural (Robertson, Wise & Blake 1993) and physiological (Draycott *et al.* 1998) development. Therefore, we need to adjust rearing methods to mitigate these deficiencies by creating an environment that promotes survival skills. However, in doing so, we need to ensure that these novel techniques do not compromise welfare during captivity. We concentrated on two facets of development likely to impact on post-release survival in pheasants: the complexity of their rearing habitat, specifically the provision of a third dimension in the form of perches to encourage roosting behaviours; and the complexity of their diet, likely to influence their propensity to forage efficiently, utilise a diversity of foods post-release and have a digestive system capable of processing a varied diet.

Roosting at night is an essential behaviour for ground dwelling galliformes (Wood-Gush & Duncan 1976), particularly as the fox is the predominant predator for released pheasants (Robertson 1988; Brittas *et al.* 1992; 2010). At around three weeks of age, wild- reared chicks start to learn roosting behaviour from their mother who promote climbing and flying to roosts with the use of calls (Collias & Joos 1953). In captivity, chickens (*Gallus gallus domesticus*) reared with access to perches had higher propensity to perch as adults (Gunnarsson *et al.* 2000) and more crucially to roost on elevated perches at night (Olsson & Keeling 2000). Exposure to perches during development influenced the physiological development that will aid prolonged perching such as stronger leg bones (Hughes *et al.* 1993; Shipov *et al.* 2010). Having access to perches also promotes flight and therefore the flight muscle development (Robertson, Wise & Blake 1993). This is also influenced by young birds performing wing-flapping behaviours to help balance on small perches (Pickel, Scholz & Schrader 2010). Having the propensity to perch and having the ability to fly up to high perching sites, combined with the physiology to hold on for extended periods of time is important for survival, and poor roosting behaviour has been linked to the high mortality observed in cheer pheasants (*Catreus wallichi*) (Garson, Young & Kaul 1992) and the grey partridge (*Perdix perdix*) (Dowell 1990). In addition to the behavioural and physiological developments, a spatially complex rearing environment can influence brain development (Marchetti & Nevitt 2003; Kihslinger & Nevitt 2006) and the ability to use three dimensional spaces (Gunnarsson *et al.* 2000; Wichman *et al.* 2007). The provision of perches in captive chickens has shown to have welfare advantages, with birds reared with access to perches being subjected to reduced aggression (Cordiner & Savory 2001; Donaldson, Ball & O'Connell 2012), as a function of less density at the ground level (Oden, Keeling & Algers 2002). However the use of perches in commercial pheasant rearing systems is seldom seen. This could be due to the observation in chickens that the risk of collisions leading to keel damage, bone

malformation and death may be manifest in reared pheasants (Gregory *et al.* 1990; Appleby, Smith & Hughes 1993), particularly as this is more profound in young birds developing their flight (Vits *et al.* 2005). However keel malformation is typically profound in egg laying hens that have diminished nutrient reserves (Tarlton *et al.* 2013) and may not be relevant for pheasant chicks. A secondary reason is that game keepers like simple uncluttered conditions to work and perceive perches as hindrances to their movements around their rearing pens.

Many aspects of foraging behaviour including food discrimination, preference and handling skills require previous exposure (Kitchener 1999; Thornton & McAuliffe 2006). In addition, the gut is highly plastic and changes with diet (Leopold 1953; Moss 1972). Pheasant are omnivorous (Hill & Robertson 1988j), and wild chicks will solely eat insects for the first three to four weeks of life (Dalke 1937; Warner 1979). However, typical pheasant rearing systems involves a mono-specific pelleted diet, *ad lib*, and in excess (Hill & Robertson 1988j; Ferretti *et al.* 2012). Foraging, diet and gut morphology work as a complex nutritional complex (Thomas 1987), therefore restricting one or more of these aspects through precluding individuals to a naturalistic diet may be the reason why released pheasants have a poorly developed foraging behaviour in the wild (Brittas *et al.* 1992; Robertson 1997; Sage & Robertson 2000). Rearing birds with natural food, even though nutritionally equivalent to commercial diet may: 1) increase the chances of learning discrimination skills; 2) develop a gastro-intestinal system that is better able to cope with wild diet; 3) learn important foraging skills; and 4) lead to a foraging behaviour that is optimal for the wild and therefore increases chances of survival. A more naturalistic diet has the potential to increase welfare prior to release. Promoting foraging to a level that would be seen in the wild through use of a more complex feeding regime can reduce time conducting frustrations and boredom behaviours (Johnson, Patterson-Kane & Niel 2004). Also the provision of a more natural diet allows for more dietary choice, this is important as it allows captive animals

to maintain homeostasis, but also reduces stress (Manteca *et al.* 2008). However, the provision of a more naturalistic diet has the potential to compromise welfare. The provision of a resource that can be monopolised may increase aggression and competition. In intensively reared galliformes, birds that obtain water via a bell drinker were subjected to more agonistic interactions than birds reared with a more equally distributed nipple drinkers (Zimmerman *et al.* 2006; Gilani, Knowles & Nicol 2013). If food provision can be monopolised we may see an uneven distribution of essential nutrients, these hungry individuals often exhibit increased stress behaviours (Rushen 2003).

Increasing complexity of habitats may reduce opportunity for aggression and hence ameliorate stress, whereas increasing complexity of diet may instigate additional competition for favoured food items and hence exacerbate stress. Results of direct aggression in terms of physical injury can be easily observed, but more subtle behavioural indicators of poor welfare require closer inspection. A barren environment does not have the features necessary for animals to perform its natural behavioural repertoire (Clubb & Mason 2003). The prevention of performing these behaviours can increase coping mechanisms, frustration and stress (Dawkins 1988; Mason, Cooper & Clarebrough 2001). Chickens exhibit increased coping mechanisms such as increased stereotypical pacing and preening displacement when they are thwarted access to naturalistic feed, nesting, incubation and sexual activity (Duncan & Wood-Gush 1972a; Duncan & Wood-Gush 1972d; Olsson & Keeling 2000). Aggressive pecking is often used by pheasants to establish hierarchies and to monopolise access to resources (Hoffmeyer 1969) and reduces important components of welfare in intensively reared galliformes (Savory 1995; Webster 1995). Aggression is such a serious problem in captive pheasant populations that many rearing farms resort to the using supressing drugs or mechanical devices such as bits and masks to reduce its effect (Butler & Davis 2010; Ferretti *et al.* 2012), these unfortunately treat the symptoms rather than

addressing the causes (Nicol *et al.* 2013).These aggressive interactions can cause reduction in psychological welfare (de Haas *et al.* 2010) as well as causing physical damage and death (Savory 1995). Good psychological welfare in galliformes can be identified by prolonged bouts of comfort behaviours (e.g.preening, wing flapping, dust bathing) (Nicol *et al.* 2009; Nicol *et al.* 2011) and suggests a state of relaxation (Spruijt, Van Hooff & Gispen 1992; Zimmerman *et al.* 2011).

We will utilise the pheasant rearing system to provide a large sample size and multiple replicates of manipulated rearing conditions that differ in their levels of enhancement necessary to improve post-release survival, specifically in the form of increased habitat complexity with the addition of perches and increased dietary complexity. We will compare behavioural indicators such as preening, aggression, mortality and preening displacement behaviours between rearing conditions in order to determine if these conditions affect the welfare of the animals prior to release.

4.2. METHODS

4.2.1. Pheasant rearing

Pheasant chicks were reared in 2012 and 2013 on the Middleton Estate, Hampshire. In each year, nine hundred one day old pheasants were purchased from a commercial supplier. Chicks were marked using individual numbered plastic patagial wing tags (Roxan Ltd) and randomly allocated to treatment groups. In 2012 three dietary treatments were applied each with 10 replicate groups, with each group comprising 30 birds, thus rearing 300 birds in each treatment. In Treatment 1, a control, chicks were reared on standard rearing crumb. In Treatment 2, chicks were reared on the standard crumb with additional 5% commercial mixed seed (Premium wild bird seed mix composing of wheat, cut maize, black sunflower seeds, naked oats, red dari,

kibbled peanuts, yellow millet, white dari, red millet, pinhead oatmeal, canary seed, safflower seed, hempseed and raisins). In Treatment 3, chicks were reared on standard crumb with additional 1% live mealworms. In 2013 two dietary treatments were applied each with 15 replicates of 30 chicks. In Treatment 1, a control, chicks were reared on standard rearing crumb. In Treatment 2, chicks were reared on standard chick crumb plus a combination of the supplements from 2012, with mealworms (1%) and mixed seed supplement (5%). All chick crumbs were commercial (Sportsman game feeds), age appropriate and provided *ad lib* and in excess. In addition, in 2013, we also applied three treatment groups differing in their access to perches. In treatment 1, a control, chicks were reared under standard commercial rearing conditions with no access to perches. In treatment 2, chicks were reared under the same standard conditions as the control treatments but with access to natural perches, in the form of hazel (*Corylus avellana*) boughs. In treatment 3, chicks were reared under the same standard conditions as the control treatments but with access to artificial perches, in the form of plastic conduit piping. The diameters, lengths and height from the ground of perches was standardised, see chapter three. Water was available *ad lib*. Each group of chicks were housed separately in a heated shed (1.3m x 1.3m) for the first two weeks and for the next five weeks they had access to an open grass run (1.3m x 6.8m) as well as the shed. Birds were in visual but not auditory isolation from other replicates throughout. To maintain stocking density, any bird that died during the rearing period was replaced by a sex-matched individual. Replacement chicks were excluded from subsequent analyses.

4.2.2. Measuring mortality

Birds were visually checked three times a day. Any birds which died were removed from the pen and cause of death was determined. There is frequently a high death rate between three and six days of age when the chick needs to make the

transition between obtaining nutrients from the yolk sac to being able to obtain nutrients from the consumed pelleted food. Birds unable to make this transition will die because of a physiological deficiency unrelated to either of our interventions. Therefore, we only included birds that died after day 6 for our analyses.

4.2.3. Measuring behavioural welfare indicators in captivity

In both years we used a continuous focal follow from randomly chosen birds from all houses, for all weeks of the study (see table 4.1). Birds were individually identified by their patagial wingtags. Each bird was only observed once. We measured the total time we watched the birds, the amount of time spent conducting preening behaviours, the number of agonistic interaction and the number of stereotypical preening-displacement behaviours. Comfort behaviours included preening, wing-flapping and dust bathing behaviours. Aggressive interactions included aggressive pecks, fights and chases directed towards or received by the focal individual. Stereotypical preening displacement was determined as a single peck directed towards parts of the body that are easily reached, usually a direct peck towards the chest (Duncan & Wood-Gush 1972a), this was easily distinguishable from a positive preening bout.

Table 4.1. Number of male and female continuous focal follows for each week the birds were in captivity for years 2012 and 2013.

2012			2013		
Week	Male	Female	Week	Male	Female
1	30	30	1	30	30
2	30	30	2	29	30
3	26	28	3	27	30
4	27	23	5	29	29
5	30	30	6	30	29
6	30	28	7	19	19

We used a generalised linear mixed model (GLZMM) to ask if the percentage of time performing comfort behaviours and the combined number of aggressive interactions per bird per hour differed with rearing treatment, sex and age as variables, and house as a random factor. We initially built a full model with all likely explanatory variables including all possible two-way interactions. Terms were then sequentially dropped until the minimum adequate model (lowest Akaike's Information Criterion) contained only variables whose elimination would reduce the explanatory power of the model. *Post-hoc* pair-wise comparisons were conducted on all significant results.

4.2.4. Ethical note

All birds were reared using commercial procedures that adhere to the DEFRA Code of Practice for the Welfare of Gamebirds Reared for Sporting Purposes (DEFRA 2009). All observations were conducted from a distance using binoculars. The work

was approved by the University of Exeter Psychology Ethics Committee and conducted under a Home Office licence number PPL30/2942.

4.3. RESULTS

4.3.1. Mortality

Our levels of mortality, excluding birds that died in their first six days, were fortunately too low (2012: 0.005%; 2013: 0.008%) to permit analysis of whether experimental rearing conditions affected deaths. In 2012, only five birds died (mealworm group = 1, control = 1, mixed seed = 3) and in 2013 only eight birds died (mixed diet = 4, control = 4).

4.3.2. Aggression

When we considered changes in aggression over time, controlling for inherent changes in aggression as the birds grew and were able to access increasing space as runs and grass pens were opened up, we continued to find that addition of perches reduced levels of aggression, whereas differences in diet did not affect aggression. In 2013, the most efficient model of aggression showed that birds reared without access to perches were subjected to higher combined aggression per bird per hour than birds reared with access to perches (GLZMM: Perches: $F_{1,269} = 4.24$, $p = 0.041$ (Figure 4.1). In 2012, the most efficient model of aggression only included week (GLZMM: Perches: $F_{1,340} = 32.44$, $p < 0.041$), with aggression decreasing as the birds got older (Table 4.2).

Table 4.2. Results from the most efficient model as indicated by AIC values. All models are GLZMM controlling for house as a random effect. Significant predictors are in bold face.

Response	*Year*	*Factor*	*df*	*df(error)*	*F*	*p*
Combined aggression per bird per hour	2012	**Week**	**1**	**340**	**32.44**	**< 0.001**
	2013	**Perches**	**1**	**269**	**4.24**	**0.041**
Comfort behaviour (%)	2012	Sex	1	332	0.14	0.712
		Diet	**2**	**332**	**4.16**	**0.016**
		Week	**1**	**332**	**38.57**	**<0.001**
		Sex*Diet	2	332	0.78	0.456
		Sex*Week	1	332	0.09	0.762
		Diet*Week	**2**	**332**	**10.62**	**<0.001**
	2013	**Week**	**1**	**269**	**38.50**	**<0.001**

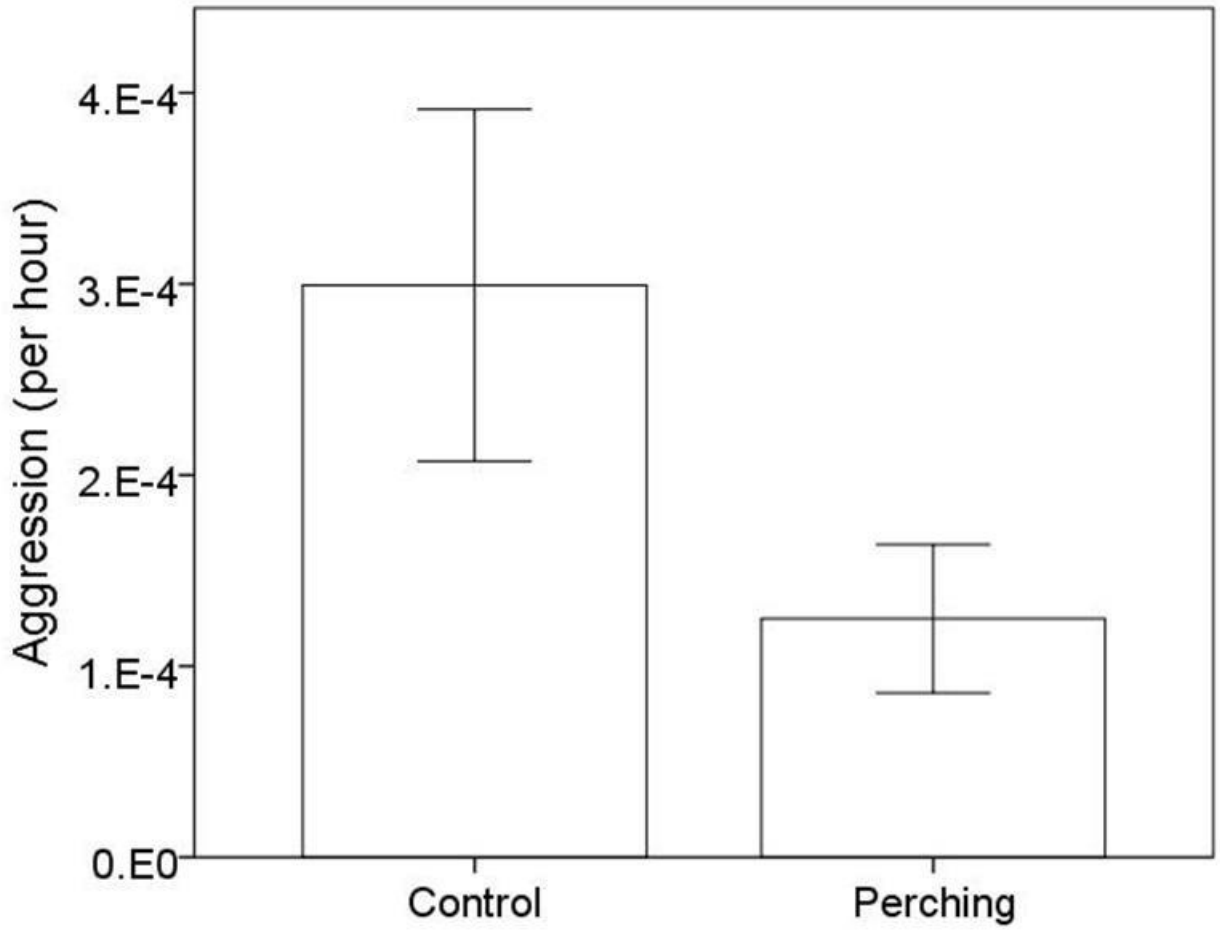


Figure 4.1: The average combined aggression per bird per hour for birds either reared with access to perches or with no access to perches in 2013. Error bars indicate 1SE.

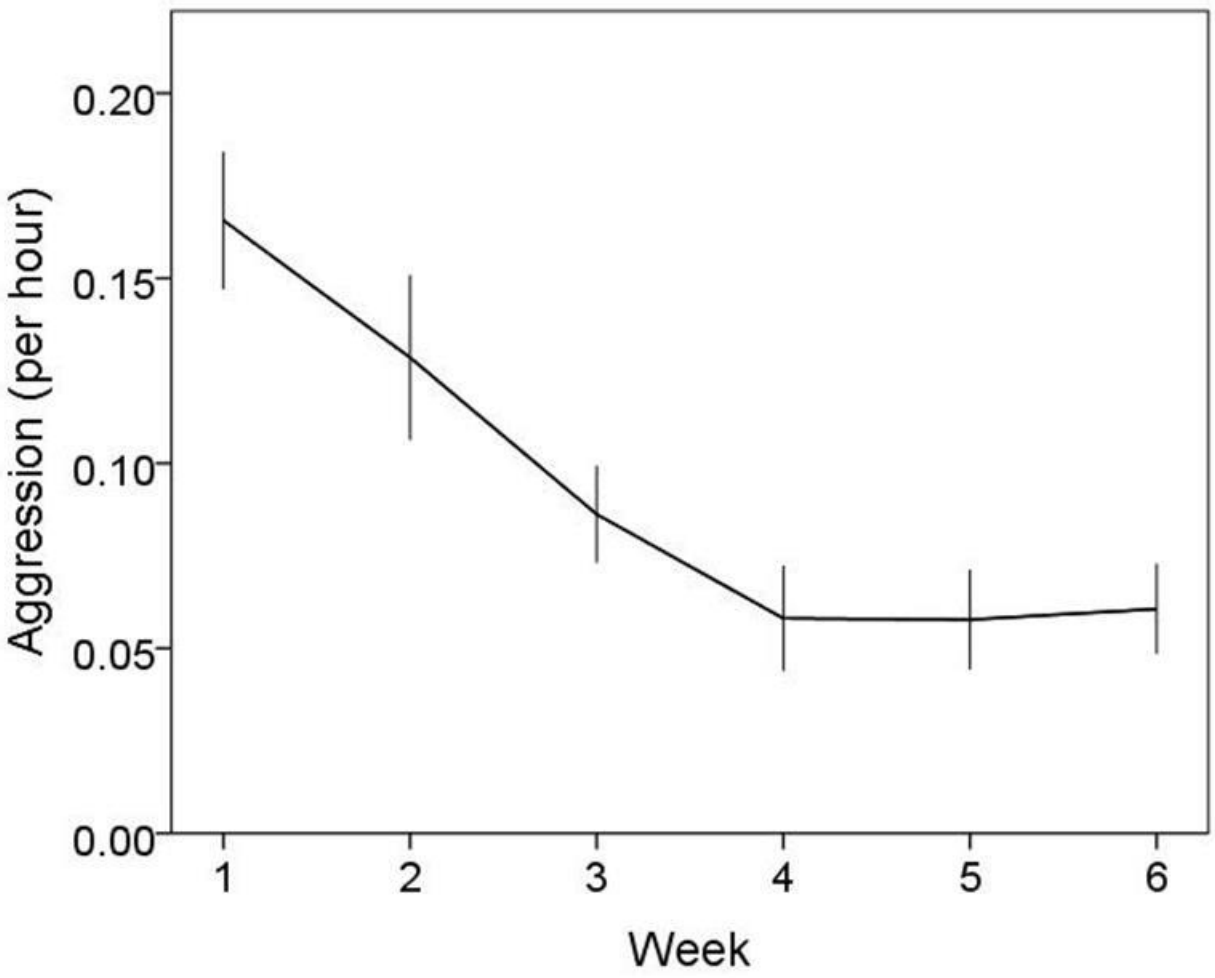


Figure 4.2 The combined aggression per bird per hour for birds reared across treatments for each week the birds were in captivity in 2012. Error bars indicate 1SE.

4.3.3. Comfort behaviours

The addition of mealworms in 2012 led to increased levels of comfort behaviours compared to control and mixed seed treatments (Figure 4.3), with the effect becoming stronger as the birds got older (Figure 4.4) (GLZMM week: $F_{1,332} = 38.57$, $p < 0.001$; GLZMM diet: $F_{2,\ 332} = 4.16$, $p = 0.016$; GLZMM week*diet: $F_{1,332} = 10.82$, $p < 0.001$). The addition of perches in 2013 did not alter the time spent performing comfort behaviours, but as in 2012, time spent performing comfort behaviours increased as the birds got older (GLZMM week: $F_{1,260} = 38.50$, $p < 0.001$; GLZMM perching: $F_{1,260} = 1.07$, $p = 0.30$; GLZMM week*perching: $F_{1,260} = 2.63$, $p = 0.11$).

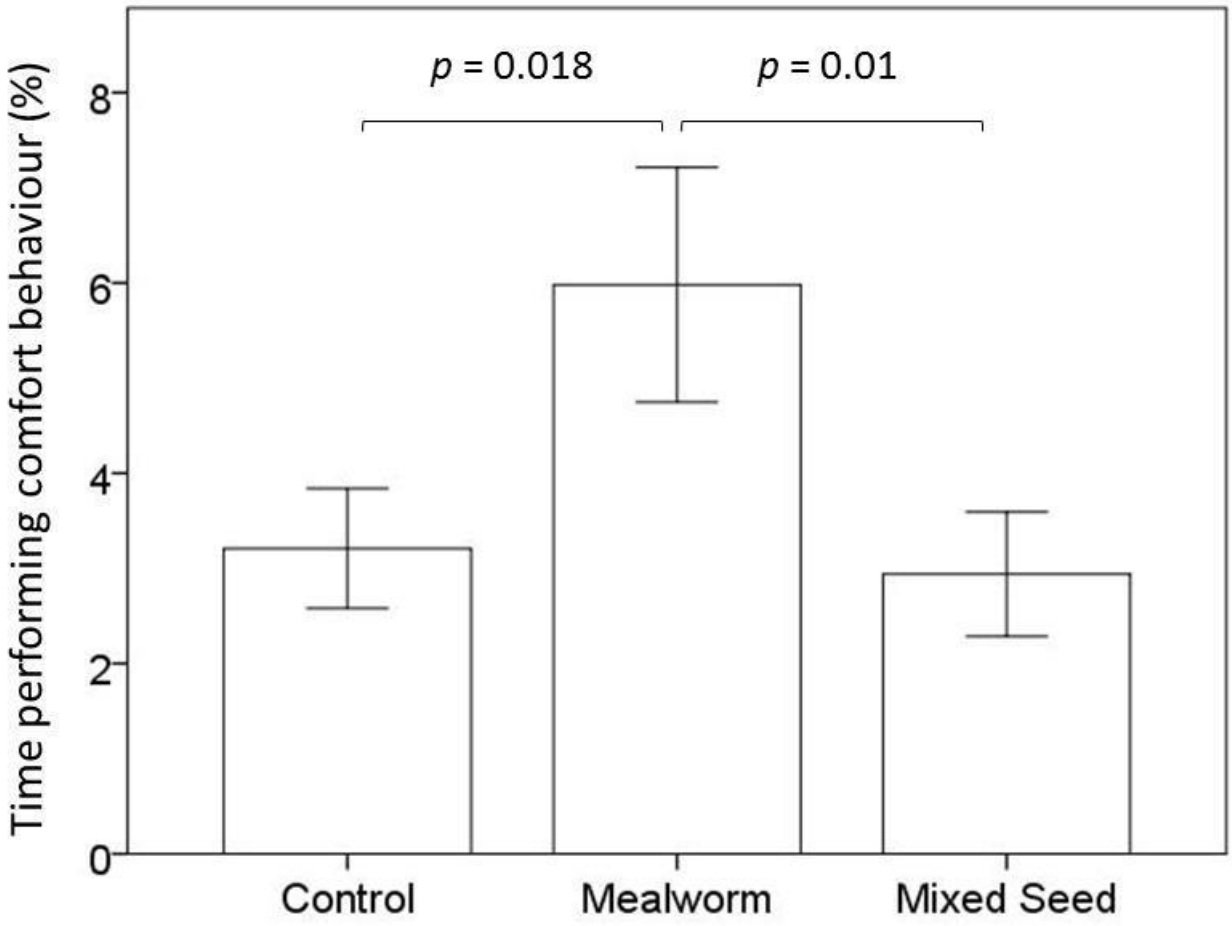


Figure 4.3 The average percentage of time comfort behaviours were performed by birds reared fed with supplementary mealworms, supplementary mixed seed and the control group which was fed solely on commercial chick crumbs. Error bars indicate 1SE.

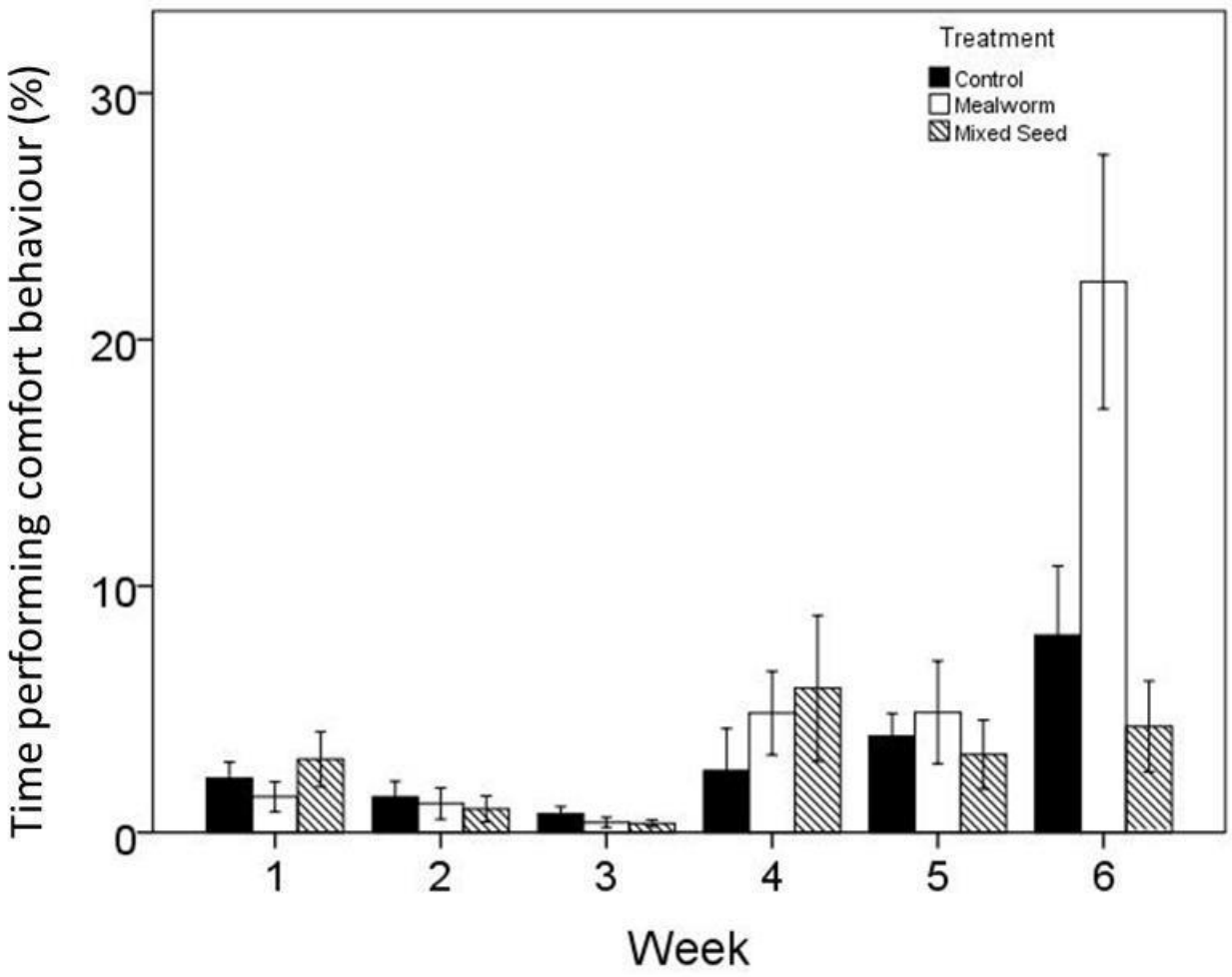


Figure 4.4 The average percentage of time comfort behaviours were performed by birds reared fed with supplementary mealworms, supplementary mixed seed and the control group which was fed solely on commercial chick crumbs for each week the birds were in captivity. Error bars indicate 1SE.

4.3.4. Displacement preening

We only saw one displacement preening behaviour in year one and two displacement preening behaviours in year 2. These low figures did not permit detailed analysis.

4.4. DISCUSSION

Rearing pheasants in environments to promote the development of important survival characteristics such as foraging efficiency, prey handling skills, and roosting behaviour did not have a negative effect on important components of welfare. Instead we saw an improvement in welfare, where the provision of environmental enrichment in the form of elevated perches reduced aggression and enhanced dietary complexity increased the amount of time an individual spent performing comfort behaviours.

Our provision of a more naturalistic diet during early development, with the primary aim of influencing physiological and behavioural developments that aid foraging behaviour and survival after release into the wild, did not compromise welfare during the captive rearing period. The provision of a highly defendable resource, such as our supplemented mealworms and mixed seed, did not increase aggression compared to birds reared with only chick crumbs. This is reassuring, because such an addition had the potential to provoke increased aggression. Aggression around a defendable resource is often high (Zimmerman *et al.* 2006; Gilani, Knowles & Nicol 2013) for instance the provision of localised feeding station in captive reared chum salmon (*Onchorhynchus keta*), increased frequencies of agonisitic interactions compared to fish reared with a scatter feeding system (Ryer & Olla 1995). A consequence of increased aggression or the resultant disproportionate distribution of food have been shown to lower welfare of birds excluded from the resource (Rushen 2003). In this study we found the opposite effect. The addition of mealworms promoted the time spent performing comfort behaviour, particularly as birds got older. Prolonged performance of comfort behaviours is an important indicator or good welfare (Spruijt, Van Hooff & Gispen 1992; Nicol *et al.* 2009; Zimmerman *et al.* 2011). Increased time performing comfort behaviours have also been observed in captive animals provisioned with a more naturalistic environment, for instance more preening behaviours were

observed in pigs that were housed in enriched environments than those reared in barren pens (Bolhuis *et al.* 2005; Bolhuis *et al.* 2006). Chickens perform more comfort behaviours in preferred environments (Nicol *et al.* 2011). It is important to note here that displacement behaviours, such as displacement preening was not confused with preening, a comfort behaviour, as these behaviours indicate frustration (Duncan & Wood-Gush 1972a). One of the reasons for an increase in time spent conducting comfort behaviours could be related to the mealworms offering more dietary choice. Restricted diet can cause physiological and behavioural parameters indicative with stress, and therefore can influence animal welfare (Manteca *et al.* 2008). For instance, domestic sheep (*Ovis aries*) fed with restricted dietary breadth showed greater blood cortisol levels, greater neutrophil to lymphocyte ratio and lower number of platelets than conspecifics reared with greater dietary diversity, whilst also exhibiting reduced intake and greater activity; factors associated with stress in sheep (Catanese *et al.* 2013). However if this was the case, it does not explain why we did not see the same levels of preening in birds reared with mixed seed diet, or even when we combined the mixed seed and mealworms treatment in the second year of the study. Exposure to increased dietary breadth may also allow individuals to avoid nutritional imbalance by choosing complementary feed as they would typically do in the wild (Provenza *et al.* 2003). The mealworm treatment, closely relates to forage in the wild where for the first 3-4 weeks a chick's feeds solely on insects, after this the birds gradually opt for a diet to include plant material including seeds (Dalke 1937; Warner 1979).

Although chicks in captivity are provided with an age and nutrient specific diet, this may provide the birds with the requirements to develop physically, even the weaker individuals (Ferretti *et al.* 2012), but we believe that the birds obtain more than just a nutritional benefit from a more naturalistic diet in terms of improvements in important components of pre-release welfare and post release foraging ability and survival (see Chapter two).

Our provision of elevated perches can influence physiological, behavioural and cognitive developments that may result in a better antipredator behaviour, better spatial awareness and better survival after release into the wild (Chapter three). It also improved the welfare of the birds during their time in captivity. Birds reared with access to perches suffered from less aggression than control birds. A similar reduction in aggression was observed in a captive chickens with access to perches (Cordiner & Savory 2001; Donaldson & O'Connell 2012), with the perches acting to lower the stocking density at the floor level (Oden, Keeling & Algers 2002) and to act as a refuge (Olsson & Keeling 2000). Increasing habitat complexity may take many forms in addition to simply adding perches. Adult pheasants, kept for breeding purposes also showed less aggression when reared with visual barriers. Pheasants used these barriers as a refuge, but also as a perching stand (Deeming, Hodges & Cooper 2011). The provision of perches did not influence the time spent conducting comfort behaviours of pheasants. Therefore animals that are reared with perches will not only have higher standards of welfare prior to release, they will also have the physiology, behaviour and cognitive ability to survive better in the wild. Given these benefits, why are perches not habitually added to rearing pens? One explanation is that the use of perches in intensive poultry systems is often neglected because of perceived risk of collisions (Gregory *et al.* 1990; Appleby, Smith & Hughes 1993). During our study we did not observe any collisions of birds trying to fly up to perches and only one bird died during the study due to a broken neck, but it occurred when flying into the mesh door.

Aggression among pheasants (and other poultry/gamebirds/galliformes) during artificial rearing is frequently high and leads to substantial injury and death (Millman, Duncan & Widowski 2000; Prieto *et al.* 2012). In many rearing systems, mechanical devices are used to reduce the effects of aggression rather than treating the issue causing the events (Nicol *et al.* 2013). Ferretti *et al.* (2012) stated that the use of

devices or drugs to control pecking in a pheasant environment should be forbidden. Although 'bitting' provides a useful tool in halving the number of bird-on-bird pecking, there are still welfare issues with increased head shaking, scratching, inflammation of the nostril and bill malformation (Butler & Davis 2010). These unnatural devices also block the field of view which inhibits the learning and behaviour (Ferretti *et al.* 2012). This study was conducted on birds at a lower density that would be seen on pheasant rearing farms. Aggression increases with stocking density (Nicol *et al.* 1999) and because access to perches lowers the density on the ground floor (Oden, Keeling & Algers 2002), combined with the reduction in aggression observed in this study, we feel that the provision of perches is an effective, simple and cheap tool to help alleviate the issues causing aggression in pheasants even at higher densities. However, more research should be conducted. If this benefit can be transferred to systems with larger numbers, analogous with numbers traditionally used in the pheasant rearing industry, then it will create ethical and financial benefits. The application of a 'bit' requires all birds to be caught at around 3-weeks old and then re-caught prior to release to remove them. If this procedure is not needed then we expect to reduce the stress associated with the application, the stress and injury associated with wearing the device, and we will stop the loss of development associated with wearing the device. Financially, this will save money on labour and the costs applying bits to 35 million birds in the UK each year.

The provision of a more naturalistic environment may directly promote the development of important skills for post release survival (Chapters two and three), and reduce physical injury from aggression, but perhaps less obvious is the indirect effects that the accompanying reduction in stress may lead to more effective neural and cognitive development (McEwen 1999; McEwen 2008; Buchanan, Grindstaff & Pravosudov 2013). Reduced stress, manifested in lower levels of circulating cortisol, may enhance performance across a suite of behaviours essential for survival post-release (Cam, Monnat & Hines 2003; Teixeira *et al.* 2007), reduce load on an immune

system (Hill 2011) and enhance nutrient assimilation from the diet (Deng *et al.* 2012). This complex interplay between early life exposure to stress and the expression of adult behaviours is often complicated and requires deeper study in this system.

We have found that two simple environmental manipulations of the early rearing environment of pheasants improves important components of welfare prior to release, but this does not mean that all enrichment devices used to help the development of survival traits will always increase welfare. The development of anti-predator behaviours through conditioning procedures can cause fear and distress (Rabin 2003), or the localisation of food to promote conflict can increase aggression, often to an unacceptable level (Stahl & Kaumanns 2003). The increase in empirical studies in reintroduction biology looking at efforts to improve post release survival are to be welcomed, but it is important to consider the welfare implication of these manipulations for the animals in captivity and under the care of humans. Such considerations should include not just immediate effects of the manipulation on injury or stress, but should also consider downstream effects mediated by altered exposure to stressors early in life at critical periods of development. We hope that reintroduction biologists who manipulate the captive environment to promote post release survival will follow this lead and start to document not only the results of the post-release program, but also detail the welfare effects prior to release.

Chapter Five

Dispersal and mortality: how personality can influence the success of restocking programs

ABSTRACT

Reintroduction and restocking programmes often fail in their efforts to create a self-sustaining population. A reason for this is individual behavioural deficiencies in antipredator behaviour and excessive movement, which increase likelihood of mortality upon release. Individual differences that are consistent across time and context are known as personalities and understanding how these personalities are affected by ecological pressures is important when trying to create a successful release strategy.

We assayed the personality of 407 hand-reared pheasants, *Phasianus colchicus*. We used a PCA to place individuals on a continuum of bold/sociable to shy/unsocial. The birds were then released into the wild and we followed their fate and dispersal for eight months. Pheasants that dispersed from the release site were disproportionately shyer and less social than the original population PCA mean. Pheasants that died on the release site of natural causes were also shyer and less social than the original population PCA mean. The remaining population that were recorded when shot on the release site did not differ from the original population PCA mean.

For conservation programs in general, the use of a high density release programme or constant restocking may cause dispersal of individuals with shy and less social personality traits. This causes a personality bias in the remaining stock. Simply restocking the release site to mitigate the dispersal will continue skewing the composition of personality within the population and new release methods using release sites that accommodate all personality traits are recommended.

Continual breeding from survivors on commercial pheasant shoots may lead to skewed personality distributions with especially shy birds making establishment of a resident breeding population difficult. We suggest a number of release mechanisms that would aid the survival of a diverse range of

behavioural types that are essential for the production of a self-sustaining population in a fluctuating environment.

5.1. INTRODUCTION

Reintroduction and restocking programs are essential for the conservation of many endangered animals (Fischer & Lindenmayer 2000). However these forms of translocation often suffer from poor success (Griffith *et al.* 1989; Kleiman 1989; Wolf *et al.* 1996), in terms of failing to create a self-sustaining wild population (Jule, Leaver & Lea 2008). Animals in restocking programs are often reared in captivity and then released into the wild in large numbers (e.g. grey partridge (*Perdix perdix*) (Buner & Schaub 2008)). Immediately after release there is a period when an animal explores novel environments and potentially encounters unfamiliar conspecifics and predators (Stamps 2007; Stamps & Swaisgood 2007) resulting in high mortality (Kleiman 1989; Brittas *et al.* 1992; Fischer & Lindenmayer 2000).

Behavioural deficiencies in the released population compared to their wild conspecifics are believed to be a major cause of mortality (Kleiman 1989) with released animals showing poor individual predator detection and avoidance (Griffin, Blumstein & Evans 2000) and poor food acquisition and processing skills (Ellis *et al.* 2000). Dispersal from the release area also influences the success of a translocation programme (Armstrong *et al.* 2013). Dispersal can take three phases which include leaving the natal site, travelling between sites and settling in the new location (Clobert *et al.* 2009; Cote *et al.* 2010). Factors driving these phases can include, mate choice, territory choice, predation risk, intraspecific competition, kin selection and habitat risk (Bowler & Benton 2005; Ronce 2007; Bernard & McCauley 2008; Clobert *et al.* 2009). Captive reared animals that are released into the wild show higher dispersal distances than would normally be expected by their wild conspecifics (Stamps & Swaisgood 2007). This not only increases the risk of entering novel environments and predators (Linklater & Swaisgood 2008), but it also diverts time and energy away from other important survival skills such as procuring shelter (Shier 2006). Ultimately, high mortality and dispersal rates reduce the size of the founding population and also reduce the likelihood of creating a self-sustaining population (Armstrong & Seddon 2008; Mihoub *et al.* 2011). Therefore, individual behaviour seems to be a central issue

with translocation programme failure and the reasons why we see animals disperse from the founder population or die within the release site need to be investigated and mitigated.

Reintroduction efficiency could be improved if released animals were assayed prior to release such that efforts could be concentrated on individuals with particular behavioural attributes, or particular mixes of individuals, which were more likely to succeed in establishing themselves as a breeding population. A series of assays specifically focussed on measuring an individual's susceptibility to predation or likely dispersal behaviour in a novel landscape is prohibitive. However, individuals typically exhibit distinct personality types which capture consistent behavioural responses across contexts and time (Réale *et al.* 2007) including general propensities to disperse or be predated. Dispersal has also been positively linked with aggression (Duckworth & Badyaev 2007), boldness (Fraser *et al.* 2001; Bremner-Harrison, Prodohl & Elwood 2004) and exploratory behaviour (Dingemanse *et al.* 2003), but negatively with sociability (Cote & Clobert 2007) but not always (see Blumstein, Wey & Tang 2009). Personality is commonly linked with mortality, with bold individuals often having a shorter life span compared to their shyer counter parts, often as a consequence of increased predation risk (van Oers *et al.* 2004; Réale *et al.* 2007; Smith & Blumstein 2008). More exploratory and active individuals have higher mortality rates (Smith & Blumstein 2008). Therefore, personality can predict ecologically relevant behaviours such as mortality, dispersal, niche expansion and social organisation (Réale *et al.* 2007) which can directly influence survival and reproductive success (Réale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Dingemanse & Réale 2005; Cote, Dreiss & Clobert 2008; Smith & Blumstein 2008). Personality is heritable (e.g. Dingemanse *et al.* 2002; van Oers *et al.* 2004), and therefore over representation of a particular personality trait can impact the long-term success of a translocation programme where the desire is to establish a viable, independent breeding population (McDougall *et al.* 2006). Although selection under one set of circumstances may favour a particular trait,

when environmental conditions change we may see a different personality trait survive better (Dingemanse & Réale 2005). Therefore, in order to create a self-sustaining population it is important to have a mixed range of personality types remaining on the release site (Watters, Lema & Nevitt 2003; Sih & Watters 2005; Watters & Meehan 2007). It is recommended that applying personality research to conservation will aid both fields (Watters & Meehan 2007). Utilising the temporal and contextual rigidity of personality allows for assaying broad personality metrics in controlled conditions early in life giving an accurate account of an individual's future behaviour in more naturalistic settings.

There is a problem with integrating reintroduction biology and personality: for many reintroduced species, animals are highly endangered with small sample sizes (Seddon, Armstrong & Maloney 2007). This makes accurate personality assessment difficult, less reliable and rare (Bell, Hankison & Laskowski 2009; Bremner-Harrison, Cypher & Harrison 2013). The shooting industry rears and releases millions of pheasants (*Phasianus colchicus*) each year in a manner analogous to conservation focussed translocation processes, with soft releases into prepared areas, habitat management and post-release care in the form of supplementary feeding, medication and predator control. Pheasants also exhibit distinct personality types with fitness consequences. Bold males were more likely to be shot early in the shooting season (4-6 months after release) whilst also having a higher likelihood of dying from natural causes, ultimately resulting in disproportionately more shy pheasants surviving the first year after release into the wild (Madden & Whiteside 2014). Although clearly not endangered, pheasants exhibit many of the individual behavioural deficiencies associated with poor success of translocation programmes described by Kleiman (1989), leading to high mortality (Hill & Robertson 1988j; Brittas *et al.* 1992; Leif 1994) and poor reproductive success (Hill & Robertson 1988a; Sage *et al.* 2003), and therefore provide a model system to explore the predictive power of personality type on individual behaviour following release into an area.

The aim of this study is three-fold. First, to utilise the advantages associated with pheasant restocking programmes to help understand how personality can influence dispersal and mortality and provide management implications of personality on future release programs in general. Second and more specifically, to add to the sparse literature on how personality influences post release pheasant survival and future reproductive success. In particular we are interested in how personality types are affected by ecological pressures related to releasing large numbers, in particular are bolder individuals likely to monopolise the core conservation area and its associated clustered resources such as supplemental feed, shelter or absence of predators (either through exclusion via fencing, or direct predator removal) or if asocial birds move to the periphery and even off the release site where such management ceases and beneficial resources are absent. Thirdly, a less obvious effect of an individual's personality is how it may affect future reproductive success mediated by morphology. Males are highly sexually dimorphic (Mateos 1998). Male secondary sexual traits such as wattles size, spur length and tail length are used in both territory acquisition and in female choice (Ridley 1983; Ridley & Hill 1987; von Schantz *et al.* 1989a; von Schantz *et al.* 1989d; Göransson *et al.* 1990; Grahn, Göransson & von Schantz 1993c). Females suffer from rapid loss of condition during the nesting season and therefore a female in better condition at the onset of the breeding season is more likely to reproduce (Draycott *et al.* 1998; Hoodless *et al.* 1999). We are interested if personality can predict morphological features that may aid a pheasant's reproductive success.

Finally, we are interested in how the impact of recreational shooting pheasants can bias the composition of surviving populations towards certain personality types and how this may affect future programmes. Given that only 16% of released birds survive to the first breeding season (Turner 2004), and these which do breed suffer from poor reproductive success compared to wild conspecifics (Hill 1985; Hill & Robertson 1988a; Sage *et al.* 2003), we could assume that the impact on the wild population (*circa* 2.3

million birds (Gibbons *et al.* 1993) would be negligible. However, this weak individual effect is offset by the number of birds released to supplement wild stock each year. Thirty five million birds are released annually (PACEC 2008), typically bred from stock from the previous year's birds that were released, survived the winter and were caught prior to the breeding season. If personality is heritable in pheasants, over representation of a particular personality type can be magnified by artificial rearing, and therefore the release of huge numbers has the potential to influence the wild population, potentially leading to evolutionary change in this game species (Allendorf *et al.* 2008).

In this study we assayed the personality of a large number of juvenile pheasants before release and followed their fate during the first eight months of their reintroduction. We tested whether particular personality traits were more likely to disperse from the release site. We specifically tested whether those dying of natural causes differed in their personality compared to the original population personality mean. Finally we asked if personality as a juvenile influenced morphological developments which might affect future reproductive success.

5.2. METHODS

5.2.1. Rearing and release

We reared and released pheasant chicks in summer 2012 on the Middleton Estate, Hampshire. The estate hosts a game shoot and employs two gamekeepers to manage the release of pheasants through habitat management, providing supplementary food, medication and water, as well as controlling predators. We purchased 900 one day old pheasants from a commercial supplier. Chicks were marked using individual numbered plastic patagial wing tags (Roxan Ltd) and randomly allocated to treatment groups. We applied three dietary treatments (as chapter 2: chick

crumb only; chick crumb plus supplemented mealworm; chick crumb plus supplemented mixed seed and fruit) each with 10 replicate groups, with each group comprising 30 birds, thus rearing 300 birds for each treatment. These treatments were balanced across birds and accounted for in statistical analysis, where it had no effect. All chick crumbs were commercial (Sportsman game feeds), age appropriate and provided *ad lib* and in excess. Water was available *ad lib*.

Each group of chicks were housed separately in a heated shed (1.3m x 1.3m) for the first two weeks and for the next five weeks they had access to an open grass run (1.3m x 6.8m) as well as the shed. Birds were in visual but not auditory isolation from other replicates throughout. To maintain stocking density, any bird that died during the rearing period was replaced by a sex-matched individual. Replacement chicks were excluded from subsequent analyses. When the birds were 5 weeks old, we took 407 birds at random from the population and assayed them using a series of behavioural tests (see below), tests previously showed to be individually consistent across time in pheasants (Madden & Whiteside 2014).

At seven weeks old, the birds from all treatments were mixed together and placed into one of two open top release pens (average pen dimensions 14400m^2) on the release site. The pens were surrounded by 2m high fences and electric wires to exclude foxes. The pen also included a large quantity of natural cover in the form of shrubs and trees, as well as artificial shelter as well as water, medicated water, and food provided *ad lib* (GWCT 1988; GWCT 1991). Birds could disperse at will from the pen and were free to roam and mix with other pheasants released on the site for recreational shooting.

5.2.2. Recovering birds

Post release and prior to the shooting season (June 2012-October 2012) we conducted daily searches of the release site. During the shooting season (October

2012-February 2013) the area was visited less frequently but more methodically as beaters, engaged in driving the game towards the waiting guns, were informed of the project and searched for carcases and tags as they walked through the site. After the shooting season (March 2013-June 2013) the same area was visited about once a week. We picked up carcasses of the pheasants that we found and identified them by their numbered wing tag. Some dead birds were damaged, indicating that they had been predated. If there was no external damage to the bird, we suspect that it died of other causes, perhaps disease. However, it is possible that birds we recovered with marks of predation had actually died of other causes and their body had been scavenged. Therefore we could not confidently discriminate natural causes of death so we combined them in to a single category of death by natural causes. Birds were shot on the release site as part of a commercial pheasant shoot. Shooting took place 16 times on the release site between October 2012 and February 2013. We recovered 49 males and 38 females shot on the release site that had previously been assayed for personality. We recovered a further 12 birds (6 males/6females) from sites other than the release site. These were supplied by neighbouring shoots, who were informed of the study. Unfortunately delay in returning means that we were unable to conduct *post mortem* analyses on these birds.

5.2.3. Collecting morphometrics

We recorded the mass of 371 birds that were personality tested on the day they were released into the wild aged 7 weeks old, using a Salter Super spring balance (precision = 10g).

We recorded a suite of morphological characteristics from 87 birds which had been shot during the hunting season (4-7months in the wild). Mass was measured using a Salter Super spring balance (precision = 10g). Tail length was measured using a steel rule under the longest tail feather (precision = 1mm); we excluded birds which had lost such feather. Average wing length was calculated from measures of the left

and right wing chord using a stopped wing rule (precision = 1mm). Mean tarsus length was calculated from measures of the left and right tarsi using callipers (precision = 0.1mm). Mean wattle area was calculated from measures of the maximum height and orthogonal width of the left and right wattles, measured using callipers. Spur length was calculated as tarsus thickness above the spur subtracted from the maximum spur length including tarsi thickness, for both the right and left spur, calculated using callipers.

5.2.4. Behavioural testing of birds

5.2.4.1. Response to a novel environment

Test one: A bird was caught from its rearing pen using a net and immediately placed into a novel environment, a plastic crate measuring 0.95 x 0.65 x 0.27m. The crate floor was covered with cardboard marked out in 20 cm squares and the crate walls were covered to ensure visual isolation. These birds were not in auditory isolation. The birds were placed in a central square and left for 1 minute. We measured the response to this environment by determining activity level, by counting the number of squares entered (including re-entries) during a one minute focal follow. A new square was entered when the outside toe of the right foot was placed in a square separate from its previous position. If the same square was left and subsequently re-entered it was counted as two. The observer watched the bird from behind a screen. Test two: conducted immediately after test one, the bird was observed again using the same methods for a second one-minute focal follow.

5.2.4.2. Response to a novel object

Immediately after test two was completed, we conducted test three where we placed a novel object (an orange ball-cock 0.05 x 0.15m, of a shape and colour not previously seen in the rearing environment) three squares away from the bird. We measured latency to touch the novel object with any part of its body (precision = 1s). If

a bird had not touched the object within three minutes, we ended the test and recorded a time of 180s.

5.2.4.3. Response to social stimuli

Immediately after test three we conducted test four where we removed one half a wall to reveal a neighbouring crate in which we placed a mixed sex group of pheasants of the same age that were unknown to the test subject. Prior to exposure we moved the test subject to the furthest square to the exposure. We then measured the time it took to place the outside toe of its right foot into the square closest to the crate. If a bird did not approach the crate within three minutes, we ended the test and recorded a time of 180s.

5.2.5. Statistical Analysis

We used principle component analyses (PCA) to collapse behavioural assays into a single component. We extracted components with eiganvalues> 1. For personality, we collapsed activity levels during test one and test two, latency to novel object in test three, and latency to conspecifics in test four.

We used a General Linear Model (GLM) to explore individual PCA personality scores, including an individual's sex, mass and rearing treatment as possible explanatory variables, and the interaction between these three main effects.

To analyse the dispersal data we separated the birds into two categories; either birds that were shot on the release site or birds that dispersed and were shot off the release site. The release site was defined as the area of continuous habitat conserved for pheasant management adopted by its keepers; an area equating to 9.05 km^2. We adopted this binary system rather than using dispersal distances because it was difficult to get accurate measurements of dispersal off the release as it involved third parties collecting the birds and returning the tags. Secondly it was difficult to determine

the exact dispersal distances of birds shot on the release site because collection of these birds involved blanketing in a large areas of land to drive the birds to the line of guns, so although we could determine where the birds were shot, the original position of the birds, on some drives, could have been within an area up to 89.53 hectares (895377m^2). We were confident that this method meaningfully separated birds that dispersed off the site from those which did not and represented the quantitative distance travelled as well as the more qualitative change in habitat management they encountered because: 1) the birds that 'dispersed' had to travel further than the maximum distance possible on the release site. The maximum possible distance a bird was able to travel from its release pen yet remain within the release site was 2 km, and the closest distance of a 'dispersed' bird was 2.7km from its release pen, the average dispersal distance of birds leaving the release site was 5.69km. This insured that there was a unambiguous divide between the two classes; 2) the birds that 'dispersed' would have walked through areas of sub-optimal habitat as there were only two shoots bordering the release site which consisted of 21.26% of the perimeter of the release site. The majority of the neighbours did not manage the land for pheasant conservation; much of the border was coniferous forest, a habitat notoriously poor for pheasant conservation (Hill & Robertson 1988j). Of the shoots that were closest to the release site, the closest 'dispersed' bird would have travelled a linear distance of 1.33 km between the outer most conservation areas of the release site to the next area of conservation connected to the neighbouring shoot. The most direct route would have required crossing two roads and a village.

We asked if the PCA personality scores of birds dying of natural causes on the release site, birds shot on the release site, and birds shot off the release site differed from the original population mean by using one-sample t-tests. We then pooled the data for birds dispersing from the release site and the birds that died of natural causes on the release site and used a GLM to ask if birds that remained on the release site

differed to those that no longer add to the founder population, including sex and its interaction of sex and fate as explanatory variables.

We used a Pearson's correlation to ask if the personality as a juvenile related to adult morphological characteristics. All analyses were conducted using SPSSv21.

5.2.6. Ethical note

All birds were reared using commercial procedures that adhere to the DEFRA Code of Practice for the Welfare of Gamebirds Reared for Sporting Practices (DEFRA 2009). For all behavioural tests, birds were in visual but not auditory isolation from flockmates for up to 5 minutes, and then in visual contact with conspecifics for up to a further 3 minutes. Released birds were attended by a game keeper. Once birds dispersed from the release pen the keepers supplied food and water. The birds were shot as part of a commercial shoot, and were not specifically shot for this study. The work was approved by the University of Exeter Psychology Ethics Committee and conducted under Home Office licence number PPL30/2942.

5.3. RESULTS

5.3.1. Placing Individuals on a Personality Scale

We extracted a single principle component score from the four behavioural measures that we collected. This explained 57.31% of the variance in the measures and had positive loading towards activity (Test 1: 0.82; Test 2: 0.91) and negative loading towards time taken to move towards a novel object (-0.72) and time taken to reach a conspecific (-0.52). Therefore an individual with a high PCA score tended to be active in a novel environment and quick to approach both novel objects and conspecifics. Such an individual could be described as bold and social. Conversely, an individual with a low PCA score tended to be less active in a novel environment and slow to approach a novel object and their conspecific. Such an individual could be described as inactive, shy and unsocial. For descriptive statistics of the tests see table 5.1.

Table 5.1. Mean performances (SEM) of males and females in each personality test

Activity	Male	Female
Mean activity in first minute (steps)	1.63 (2.84)	1.10 (0.26)
Mean activity in second minute (steps)	4.51 (0.65)	2.56 (0.41)
Time taken to touch novel object (s)	148.23 (3.96)	151.84 (3.66)
Time taken to reach conspecific (s)	1.15 (4.49)	121.22 (4.07)

5.3.2. Does personality relate to mass and sex prior to release into the wild

Pheasant PCA scores were not explained by sex, dietary condition or an individual's mass prior to release, nor any interactions between these three factors (Table 5.2).

Table 5.2. Factors predicting variation in PCA personality scores prior to release into the wild

Factor	df	$F_{df, 359}$	*p*
Sex	1	0.64	0.42
Diet	2	0.19	0.83
Mass	1	0.00	0.99
Diet*Mass	2	0.11	0.90
Sex*Diet	2	0.71	0.50
Sex*Mass	1	1.08	0.30
Sex*Diet*Mass	2	0.63	0.53

5.3.3. Does the personality PCA score relate to fate of released birds

Pheasants dispersing from the release site were shyer and less social as juveniles compared to the original population, with a PCA score lower than the original population mean (One-sample t-test: fate: t_{11} = -3.78, *p* = 0.003, 95% CI Lower = -0.63, Higher -0.17, Figure 5.1). Pheasants dying of natural causes on the release site were shyer and less social as juveniles compared to the original population, with a PCA score lower than the original population mean (One-sample t-test: fate: t_9 = -5.85, *p* < 0.001, 95% CI Lower = -0.67, Higher -0.30 Figure 5.1). This contrasts with pheasants shot on the release site who had a juvenile PCA personality scores that did not differ from the original population mean (One-sample t-test: fate: t_{86} = 0.91, *p* = 0.37, 95% CI Lower = -0.13, Higher 0.35 Figure 5.1). Birds that would no longer contribute to the founder population, (those which had died of natural causes and those that had dispersed from the release site), were shyer than the birds which remained on the release site and were shot (GLM: Fate: $F_{1, 105}$ = 4.66, *p* = 0.03). This effect was consistent across sexes (GLM: Fate*Sex: $F_{1, 105 =}$ 0.22, *p* = 0.64 Figure 5.2.).

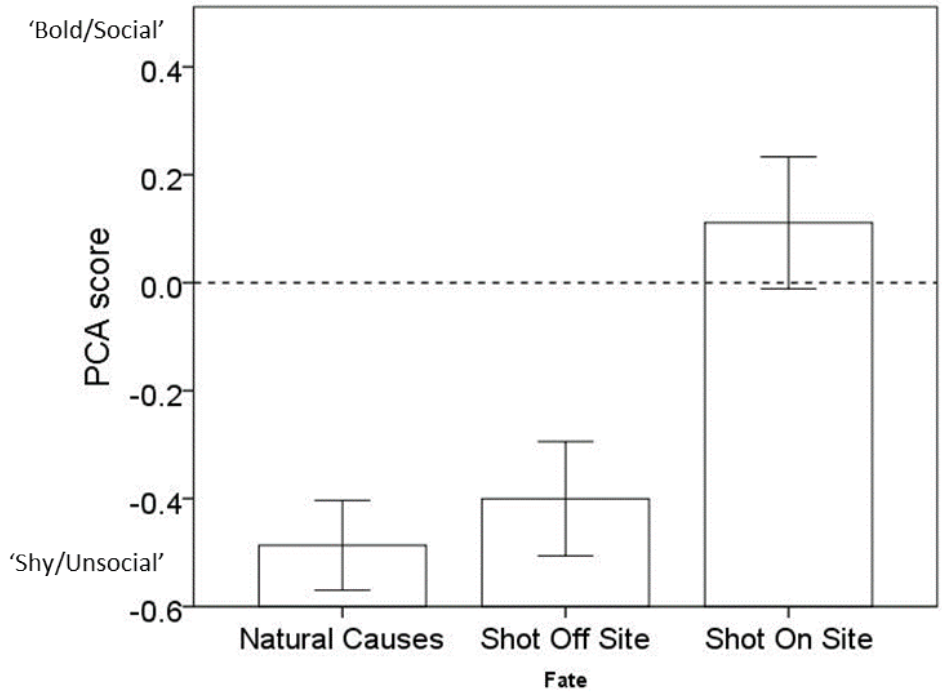


Figure 5.1. Mean juvenile PCA personality scores for pheasants that: 1) died of natural causes; 2) dispersed from the release site and then shot, and 3) remained on the release site and shot. Error bars indicate ± 1SE. The dashed line indicates the original population mean PCA personality score.

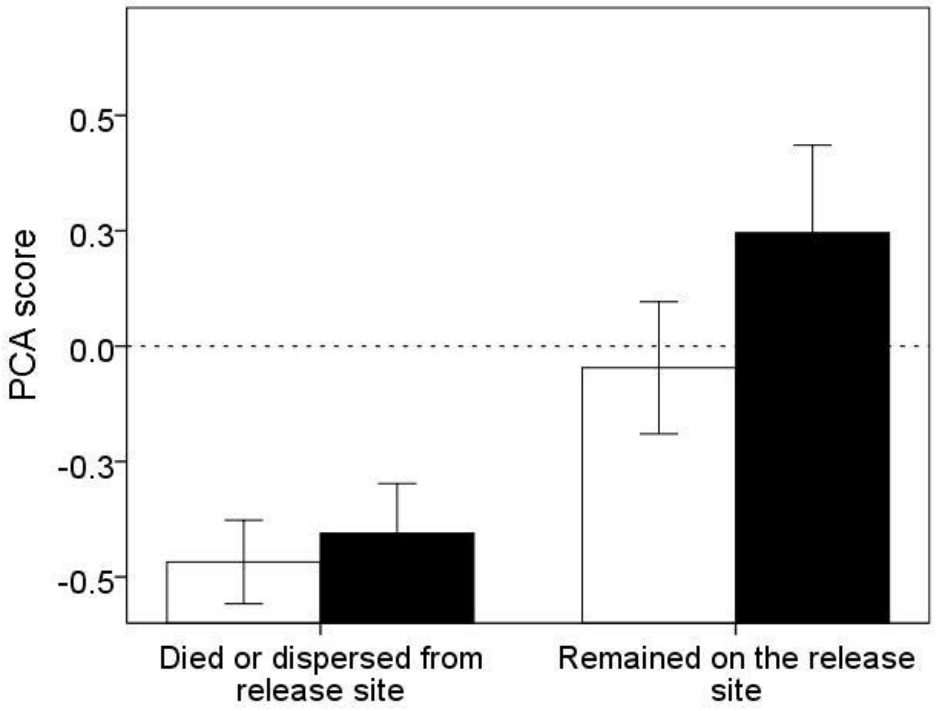


Figure 5.2. Mean juvenile PCA personality scores for males (black bars) and females (white bars) for: 1) pheasants that died of natural causes or dispersed from the release site; and 2) those which remained on the release site and shot. Error bars indicate ± 1SE. The dashed line indicates the original population mean PCA personality score.

5.3.4. Does personality relate to morphological measures of adult birds?

We found no correlation between adult morphological measures and PCA score derived from juveniles for either males or females, even before correcting for multiple comparisons (Table 5.3). For descriptive statistics of morphological measures see table 5.4.

Table 5.3. Pearson correlations between an individual's PCA score and adult morphological measures

Morphological measure		Males	Females
Tail (mm)	r	0.12	0.08
	p	0.44	0.65
	N	44	37
Mass (g)	r	0.23	-0.13
	p	0.14	0.43
	N	44	37
Mean wing length (mm)	r	0.23	0.05
	p	0.13	0.76
	N	44	37
Mean tarsus length (mm)	r	0.16	-0.27
	p	0.31	0.10
	N	44	37
Mean wattle size (mm2)	r	0.05	
	p	0.75	
	N	44	
Spur length (mm)	r	0.04	
	p	0.79	
	N	44	

Table 5.4. Mean morphometrics (SEM) of adult males and females

Morphological trait	Male	Female
Wing (mm)	260.5 (0.8)	228.9 (0.9)
Tail (mm)	466.2 (8.3)	277.0 (3.9)
Tarsus (mm)	80.79 (0.31)	70.34 (0.44)
Spur length (mm)	10.65 (0.20)	N/A
Wattle area (mm2)	1446.3 (24.6)	649.3 (17.9)
Mass (g)	1617.8 (21.3)	1223.1 (17.7)

5.4. DISCUSSION

Pheasants released as a part of an intensive restocking programme exhibited dispersal and mortality that could be predicted from their individual personality scores

assayed early in life. Pheasants that dispersed from the release site had lower PCA personality scores than the original population mean, indicating that these birds were shyer and less social. This disproportionate dispersal of shy and less social individuals is not normally expected in animals subjected to a translocation programme because dispersal is often linked to boldness and the readiness to explore novel environments (Fraser *et al.* 2001; Bremner-Harrison, Prodohl & Elwood 2004). We believe that two factors could explain why we see increased dispersal of shy and less social birds. Firstly, pheasants are released into a highly managed release site where keepers provide resource clusters of food, water and shelter (Hill & Robertson 1988j). These clustered resources can be monopolised or dominated by particular individuals and therefore shy birds, which are commonly dominated by bolder individuals could be actively forced out of the release area (Cote *et al.* 2010). Secondly, sociability is density dependent with asocial birds being most affected at high densities (Réale *et al.* 2007) and therefore individual dispersal is linked to the population density within an area (Cote & Clobert 2007). Pheasants are released in large numbers and release sites have far higher population densities than would be seen naturally in the wild. This may result in less social or shyer birds choosing to disperse from the release site.

Pheasants that died of natural causes during the shooting season were shyer and less social than the mean PCA personality score of the original set of birds that we tested and released. Typically it is bold individuals that have a high mortality rate (Smith & Blumstein 2008), often as a function of their risk taking behaviour (Réale *et al.* 2007). Our result matches that of Madden and Whiteside (2014) who found the same result at a different site, attributing the higher mortality to an increased susceptibility of shy pheasants to stress and disease (Carere, Caramaschi & Fawcett 2010). However, because we demonstrate that shyness and sociability influences dispersal of pheasants from the release site, we suspect that there is a behavioural component that could further explain this susceptibility for shy and less social birds to die from natural causes. The provision of food, medication and predator control are often localised to

specific areas of the release site, the shy and less social birds that remain on the release site may be forced out of the areas, and substantially increase their risk of dying from starvation, disease or predation.

Individual PCA personality scores may be related to morphology (Colléter & Brown 2011), such that differences observed in mortality and dispersal could actually be driven by body size or trait size. We think this is unlikely in pheasants as we found no relationship between an individual's juvenile PCA personality score and its mass upon release or its morphological traits as an adult. Therefore we believe that the differences in dispersal and mortality after release are driven by personality manifested through behavioural differences and not morphological characteristics.

5.4.1. General implications for reintroduction biology

Both the dispersal of shy and less social birds from the release site and the death from natural causes of shy and less social birds that remain on the release site has important implications for reintroduction and restocking programmes beyond game rearing and release. Dispersal and mortality can influence the number of animals remaining on the release site and consequently reducing the likelihood of creating a self-sustaining population (Armstrong & Seddon 2008; Mihoub *et al.* 2011). Reintroduction programs often alleviate the issue of dispersal by simply adding more stock to the release population (Armstrong *et al.* 2013). This method may increase the numbers that remain in the founder population, but it may also select for birds that are able to monopolise the resources of the release site or be able to tolerate high densities of animals. This over representation of a particular personality trait within a surviving population could skew group dynamics in the future. For instance, by shy and asocial birds either dying from natural causes or dispersing from the release site, the birds remaining on the release site to breed again will be disproportionately bolder and more social than the original population; this could have consequences for the following

breeding season. More social individuals remaining at the point of release may cause a density build up than may lead to increased conflict for resources and an accumulation of waste which can increase disease and attraction to predators (Banks, Norrdahl & Korpimäki 2002)..

Personality is heritable (e.g. Dingemanse *et al.* 2002; van Oers *et al.* 2004) therefore we would expect that the bolder and more social individuals that do breed on the release site will have bold offspring. This is particularly important because a successful population requires a range of personality types (Watters, Lema & Nevitt 2003), as it reduces founder effects and inbreeding depression, therefore better preparing the population for fluctuating environments (Stamps & Swaisgood 2007; Watters & Meehan 2007). Therefore, by artificially skewing the population through differential survival and dispersal, we may find that future populations survive less well particularly if environmental factors change to favour a different personality type (Dingemanse & Réale 2005).

5.4.2. Implications for pheasants restocking programmes

Unlike many reintroduction and restocking programmes, pheasants are shot, and this apparently "unselective shooting" can in fact selectively remove individuals based on personality (Madden & Whiteside 2014), and therefore influence survival, dispersal, success of the restocking programme and ultimately the evolutionary trajectory of the game species (Allendorf *et al.* 2008).

Bolder and more social pheasants are shot earlier in the shooting season (Madden & Whiteside 2014). Originally multiple reasons why these bold birds may be preferentially shot compared to shy birds in the population were suggested: the main speculation being that hunters may preferentially shoot higher and therefore 'more sporting' birds and that these flight dynamics and trajectory (Robertson, Wise & Blake

1993; Korte *et al.* 2005) may be influenced by personality. Our results here suggest that bold birds were disproportionally shot because the shy and less social birds had already dispersed from the release site meaning that only the bolder and social birds remained on the release site to be shot.

Madden and Whiteside (2014) found that disproportionately more shy birds were observed surviving the winter. We did not look at survival in this current study, but even though we saw shy and less social birds dying from natural causes and dispersing from the release site, we still suspect that we would see an overrepresentation of shy birds in the following year because: 1) In-depth studies using radio collared released populations and using data from the Game Bird Census shows that in the first year around 25% of birds die due to natural causes (Turner 2004) and over 40% of bird die from being shot (Tapper 1999; Aebischer 2003). Therefore a higher proportion of bolder and more social birds being shot compared to the shy and less social birds dying of natural causes means that an over-representation of shyer birds will remain; and 2) although we had shyer and less social birds dispersing from the release site, we believe that because bold birds are often shot earlier in the season (Madden & Whiteside 2014), there is a potential that asocial birds, that are density dependent (Cote & Clobert 2007), may start to return to these areas as competition and density is reduced. Unfortunately we did not record this in the study. The attachment of radio-collars would help identify if shy and social birds return to the release site as density reduces.

Although we found that PCA personality scores did not relate to morphological traits or secondary sexual characteristics which will influence males mating success or females ability to cope with the stress of reproduction, having an over representation of shy and less social birds in the following breeding season can still have major effects on future success and evolution. During the pheasant breeding season, game managers often stop supplementary feeding the stock (Draycott *et al.* 1998; Hoodless

et al. 1999), requiring the surviving mothers to adopt another foraging strategy and search for novel food items. Here we may expect the shy and less social pheasant to struggle to make this transition that may be easier to a bolder individual with its willingness to explore the novel environment and try new food items, as seen in Trinidad killifish (*Rivulus hartii*) and swift foxes (*Vulpus velox*) (Fraser *et al.* 2001; Bremner-Harrison, Prodohl & Elwood 2004). This could explain why we see female pheasants rapidly losing condition and exhibiting high nest abandonment compared with wild birds during the subsequent breeding season following release (Hill & Robertson 1988a; Draycott *et al.* 1998; Hoodless *et al.* 1999). A further problem is that it is common practice in pheasant restocking programmes is to catch a subset of individuals that survived the shooting season to act as captive breeders to produce stock for the following year's release. If, as seen in other species, personality is heritable (Dingemanse *et al.* 2002; van Oers *et al.* 2004), the released population the following year will be on average shyer and less social than previous years. This means that these birds will have greater risk of dying from natural causes and dispersing from the release site. This would be fine if there was no further restocking events- the shy and less social birds that survive will be able to monopolise the resources on the low density release site and can develop improved abilities to reproduce in the wild. However, the problem arises when these asocial and shy birds are subjected to annual restocking events, introducing large numbers of bold, competitive but sexually unsuccessful birds that have poor reproductive success (Hill & Robertson 1988a; Sage *et al.* 2003). The shyer birds that have survived and had prior experience reproducing cannot do well because they are displaced or disperse from the release site. Hence the continuous annual restocking of pheasants onto a release site will hamper the establishment of a self-sustaining population.

One way to counteract the over representation of shy birds observed by Madden and Whiteside (2014), and suggested in this study, would be to reduce the number of bold birds shot each year. This could be achieved in three ways: 1) test the

personality of birds prior to release and artificially select the birds to suite the release as suggested by Watters, Lema and Nevitt (2003); 2) use multiple releases on known personality composites at different times of year, e.g. release shy birds in low numbers during the early shooting season, and then supplement with bolder birds later in the year; These approaches, although robust, are unfeasible at any commercial scale because of the time, effort and expertise required to assay and discriminate huge numbers of birds. A more practicable solution 3) is to create a release site that allows birds from all personality loadings to remain during the shooting season. This can be achieved by either reducing the density that birds are released and therefore making it more bearable for asocial birds to remain on the release site or the provision of more resource locations that cannot be monopolised, such as transferring from a hopper based rearing system to a scatter feeding, whereby restricting the proportion of bold being able to dominate desired areas and actively forcing birds away. By catering for all personality types we expect that there will be equal proportions of birds to be shot, giving a more representative sample surviving the season which is important for the creation of a self-sustaining population (Watters, Lema & Nevitt 2003; Stamps & Swaisgood 2007; Watters & Meehan 2007).

5.4.3. Conclusion

Individual behaviour has important consequences for the outcome of a translocation programme. Some suggest the manipulation of release methods to include personality type compositions which may help with survival and reproductive success (Watters, Lema & Nevitt 2003; Sih & Watters 2005; Watters & Meehan 2007). However, in some systems this is not viable either because of high release numbers, or because of short time periods in captivity not allowing for suitable testing. With these programmes in mind, it may be best to use pilot studies to determine the effects personality can have on the programme (Stockwell, Hendry & Kinnison 2003) and then to create a release environment which allows for all personality types to co-exist.

Chapter Six

What limits harem size? Individual and group vigilance levels constrict opportunities for sexual skew

ABSTRACT

In harems, where choosy females collect around a preferred male offering no material benefits, it is expected that both sexes would favour larger groupings. Males benefit from access to more females; females gain group augmentation benefits including enhanced vigilance or diluted predation threat. Despite this coincidence of interest between the sexes in larger harems, natural harems are seldom especially large. We observed pheasants (*Phasianus colchicus*) to determine costs of increased harem sizes, measuring individual vigilance and foraging behaviour exhibited in groups of different sizes. From this we calculated the collective vigilance of groups. We determined the distribution of natural harem sizes in the population and searched for evidence of coercion by males and females trying to control harem size. Females reduced individual vigilance levels as harem size increased, permitting increased foraging. In contrast, males exhibited correspondingly higher vigilance levels, perhaps because of increased mate guarding, but this reduced their foraging. We observed no intra-harem aggression, suggesting that harem size was not determined by coercion. We calculated overall vigilance in groups of different compositions, concluding that maximum vigilance occurred when harems comprised one male and two females. This matches the common harem size observed in our study population. Harem size is strongly influenced by the vigilance behaviour of its constituent members. Despite a shared interest in increasing harem size, their optimal size is influenced by trade-offs in individual vigilance behaviour, resulting in relatively small harems, perhaps leading to females associating with less preferred males, and males being surrounded by fewer females than he could mate with.

6.1. INTRODUCTION

Harems, collections of females about a single male during the breeding season (Emlen & Oring 1977), pose a series of recruitment problems for their individual members. It is not clear how many females should opt to join a harem of a given size, nor how many females a male should try to recruit, and consequently what is an optimal harem size for each individual. In traditional group living models, the optimal group size is often restricted by competition for resources (Clark & Mangel 1986; Majolo, de Bortoli Vizioli & Schino 2008) and ecological constraints (Wrangham, Gittleman & Chapman 1993; Chapman, Chapman & Wrangham 1995), but these models are often restricted to the non-breeding season and fail to account for skewed patterns of attraction, frequently seen in polygynous mating systems.

Males benefit from larger numbers of females joining their own harem for two reasons. Obviously, more potential mates benefit the male through elevated reproductive success (Holm 1973), and males may gain disproportionate benefits through mate-choice copying such that large harems lead to ever greater recruitment of undecided females (Gibson, Bradbury & Vehrencamp 1991). More females also provide non-sexual benefits; by increasing group size they may provide general group augmentation benefits through increased vigilance, confusion of attacking predators, or a more general dilution effect if a predator attacks (Hamilton 1971; Pulliam 1973; Altmann, Wagner & Lenington 1977; Wittenberger 1979). Increased group size may also promote greater foraging efficiencies by enhanced information acquisition and transfer (Clark & Mangel 1984; Giraldeau & Dubois 2008). Under such conditions, males should encourage ever greater numbers of females to join their harem, either through advertisement (Verner 1964) or coercion (Bartholomew 1970; Altmann, Wagner & Lenington 1977). However, large numbers of females also produce problems for the male. An increase in numbers reduces the efficiency with which a male may guard any one of his mates against other males or predation (Knight & Temple 1988). This may cost the male in terms of his own mating success and also his

investment in guarding behaviour to the exclusion of his own e.g. foraging or vigilance behaviour (Seyfarth 1978; Packer 1979; Wittenberger & Tilson 1980; Bergerud & Mossop 1984; Hannon & Martin 1992; Alberts, Altmann & Wilson 1996). It may also impose costs on the male through increased competition over food resources when large, dense groups forage in the same area (Wittenberger 1979; Hurly & Robertson 1985; Baird & Liley 1989). Consequently, although intuitively males may be expected to strive for larger harems, there may be decreasing benefits from continued harem expansion.

From a female perspective, additional females may dilute the resources that any one male can provide her (e.g. food access (Hannon & Martin 1992), harassment defence (McBride, Parer & Foenander 1969; Ridley & Hill 1987), nesting sites (Knight & Temple 1988)), such that it becomes more beneficial to join a lone male of lower quality, than one with another female (or indeed many) in his harem, or to actively prevent other females from joining that male (Wittenberger & Tilson 1980; Yasukawa & Searcy 1982; Hurly & Robertson 1984; Hurly & Robertson 1985). In such cases, where resources are limited, females prefer to belong to small harems, or engage in simple pair bonds. However, like males (as described above), females may benefit from the presence of others in the group providing general anti-predator or information acquisition group augmentation benefits. Further, females may benefit from a dilution in the level of mate-guarding that a male can exert on them. With more females in the harem, an individual may find it easier to leave the group for copulations with other males (Ridley 1983). Consequently, the optimal harem size for any female depends on the trade-offs between these various sets of costs and benefits.

The resolution of harem size will certainly depend to some extent on the optimal balances for each member as described above, but ultimately will be facilitated by the control that each individual can exert on others as to whether they may join or remain in a harem. In species with harem-based mating systems, males are typically well-

ornamented, attracting females to them with conspicuous visual and vocal displays (Verner 1964; Ridley 1983). Males in these systems are also usually larger and better armed than females (Ridley 1983; Kelly 2006) and so can physically coerce females into joining or leaving groups (Bartholomew 1970; Altmann, Wagner & Lenington 1977). Violent determination of group membership is not restricted to males; females too can attack and drive out other female group members (Hurly & Robertson 1984; Hurly & Robertson 1985). Therefore, the realised size of a harem is determined by a complex mixture of opportunity, ability and motivations from all individual members. This makes predicting and explaining harem size difficult.

The pheasant (*Phasianus colchicus*) provides an ideal system to determine the costs of harem size on behaviour in the wild and hence to understand the observed variation in harem sizes in a population. The pheasant exhibits a system of harem defence polygyny, yet males are territorial (Taber 1949; Ridley & Hill 1987). A male acquires mates through a complex process of territory acquisition through agonistic male-male interactions, followed by courtship displays to attract hens (Ridley 1983; Mateos & Carranza 1997). The acquired territory size and quality does not seem to affect female recruitment, with secondary sexual traits such as the wattle, spur length, body size and courtship behaviours (e.g. lateral struts) being better predictors of female choice (Ridley & Hill 1987; von Schantz *et al.* 1989a; von Schantz *et al.* 1989d; Göransson *et al.* 1990; Grahn, Göransson & von Schantz 1993c). Males offer no parental care (Taber 1949), and females do not necessarily nest on the male's territory (Hill & Robertson 1988j), so males are not limited by provision of care or resources in their number of mates. Even though populations tend to have an equal sex ratio (Grahn, Göransson & von Schantz 1993c), harem size is highly skewed with only half the males in a population having attendant females and most harem-holding males having two mates or fewer (Ridley & Hill 1987). However, on some sites, average harem size may be larger (e.g. 4.9 females reported in (Robertson 1986)). Pheasants are generalist foragers, and on our study site during the early spring (as in other

studies – see Hill and Robertson (1988j)), typically forage for grains and young foliage (Lachlan & Bray 1973) on the open ground. Females are morphologically cryptic but are conspicuous when feeding gregariously in the open.

Vigilance levels in the open environments, such as fields where pheasants commonly forage, are important for survival of pheasants who typically spend large portions of their time foraging in harems prior to the start of the breeding season (Bertram 1978). Pheasants in the UK are predated by terrestrial and aerial predators, including foxes (*Vulpes vulpes*) and goshawks (*Accipiter gentilis*) (Kenward, Marcström & Karlbom 1981; Brittas *et al.* 1992) with around 25% of birds being predated in their first year (Turner 2004). We observed natural harems of pheasants prior to the start of the nesting period, and measured foraging and vigilance times in groups of different sizes. Particular males may exhibit high levels of vigilance and thus be more attractive to choosy females (Ridley & Hill 1987). Such heightened male vigilance protects the female against not only predators, but also harassment by other males (Ridley & Hill 1987). Females who are disrupted from foraging by predators or harassing males likely lose foraging opportunities. We expect that vigilant males attract larger harems, and that in larger harems, individual females can reduce their own vigilance levels, perhaps benefiting by correspondingly increasing their foraging levels. Alternatively, we may observe that additional females do not lead to increased *per capita* foraging – perhaps due to interference or competition. If this is the case, then we may expect to observe females deterring other females from joining their harem; we expect that males should strive for large harems to maximise their reproductive success. Males may also benefit from recruiting further females, benefiting from increased overall vigilance at the group level and hence reduced vigilance by the male. If this occurs, then we expect that male vigilance decreases as harem size increases. Conversely, males may pay a cost in terms of increased vigilance against competing males as his harem size increases and he invests more in mate guarding. If this occurs then we expect that male vigilance increases as harem size increases. If this leads to a corresponding decline in foraging

then we may expect to observe males deterring females from his harem through violence. With each individual contributing to vigilance in a group, we could calculate the overall level of vigilance exhibited in a group, and so determine what mix of individuals produced the maximum level of group-level vigilance. We can then assess the importance of group-level vigilance on determining harem size by comparing the sizes of observed harems in the population with the theoretical optimum harem size. By comparing vigilance levels for individuals with differing harems sizes we can determine if males are consistent in their behaviour.

6.2. METHODS

6.2.1. Study Site

We conducted this study on the Middleton Estate, Hampshire, UK (51^{0}18'N, 1^{0}4'W), between 19 March 2014 to 11 April 2014, a period when males had secured their territories but prior to female nesting. The estate hosts a game shoot and employs gamekeepers to manage the habitat, provide supplementary food, and control predators. All behavioural observations were conducted when birds were preparing for the breeding season. During this period males have established well-defined territories. The origins of many of these birds are unknown; many will have been reared and released on the estate, others will have walked in from neighbouring areas, and some reared from a wild population.

6.2.2. Behavioural Observations

81 males and 43 females were observed. All observations were conducted either during the first two hours after first light or the final two hours before last night, a period when pheasants are most active (Taber 1949). An individual was only watched once unless a known individual, either identified by territory, wing tags or distinctive marking, had a harem size that differed from its previous recording. All individuals were

observed using a continuous focal follow for a maximum of 5 minutes where the amount of time spent foraging; the number of foraging bouts; and the number of aggressive interactions, including direction of aggression, were recorded. Aggressive interactions were any behaviour that could be used by a male to coerce females into his harem, or by females to expel females or detract other females from entering the harem. These behaviours included feather pecking and aggressive pecking. We also recorded the number of incursions by neighbouring or satellite males during the focal. We used an instantaneous sampling technique with 15 second intervals to establish an activity budget. All behaviours recorded were mutually exclusive. Foraging included eating, drinking and searching for food, identified as walking with the pheasant's head and neck directed towards the ground. Vigilance was defined as when the bird's neck was extended and eyes open. Other behaviours include walking, resting and the performance of comfort behaviours which included preening and dust bathing.

Male pheasants with harems are highly territorial (Ridley & Hill 1987; Grahn, Göransson & von Schantz 1993c) and by mapping our observation points we could ensure that each male was only observed once, we also concentrated on specific areas of the estate for each trip, therefore we could guarantee that subsequent males were not the same individuals. 8 out of the 48 males with harems and 18 out of 35 solitary males had individual numbered wingtags. Females have home ranges larger than males (Ridley & Hill 1987) and will visit different males prior to nesting (Göransson *et al.* 1990), to ensure that we only watched a female once we would concentrate observations in a particular section for each trip into the field, this allowed us to know that after watching one female, subsequent females were not previously observed. Harem size was recorded for each focal individual, determined as the maximum number of hens seen within 25m of the male (Hoodless *et al.* 1999). A solitary male can either be territorial and have no females or a satellite and therefore free to roam.

Observations were curtailed in mid-April because the habitat and the height of vegetation made it difficult to determine harem size and behaviours; this coincided with the onset of early nesting (Hill & Robertson 1988j).

6.2.3. Statistical analysis

Individual behaviour was measured as a percentage of time spent performing that behaviour. Males and females were analysed separately. We used an ANOVA to determine if there was a difference in behaviour between harem sizes. We used a polynomial contrast to determine if the differences in behaviour for birds with harems were linear. A repeated measures ANOVA was used to calculate differences between harem-sizes and between individuals. From this repeatability (r) was calculated as the ratio between individual variance (s^2_A) to the total variance ($s^2_A + s^2$) (Lessells & Boag 1987).

Collective group vigilance was calculated as the mean female percentage vigilance for a specific group size multiplied by the number of females within the group with the addition of the average vigilance of a male for that same group size. To calculate optimum group size, the curve function was determined from the group vigilance plotted against harem size and the maximum group vigilance and optimal harem size derived. All models were visually inspected to ensure homogeneity of variance, normality of error and linearity. All statistics were conducted using PASW statistical software (PASW version 18, 2010, IBM, Chicago, IL, USA).

6.3. RESULTS

6.3.1. Female behaviour in the wild

Females in larger groups exhibited lower levels of *per capita* vigilance than those in smaller groups (ANOVA: Polynomial Contrast: $F_{4,38} = 5.22$, $P < 0.001$, Figure 6.1).

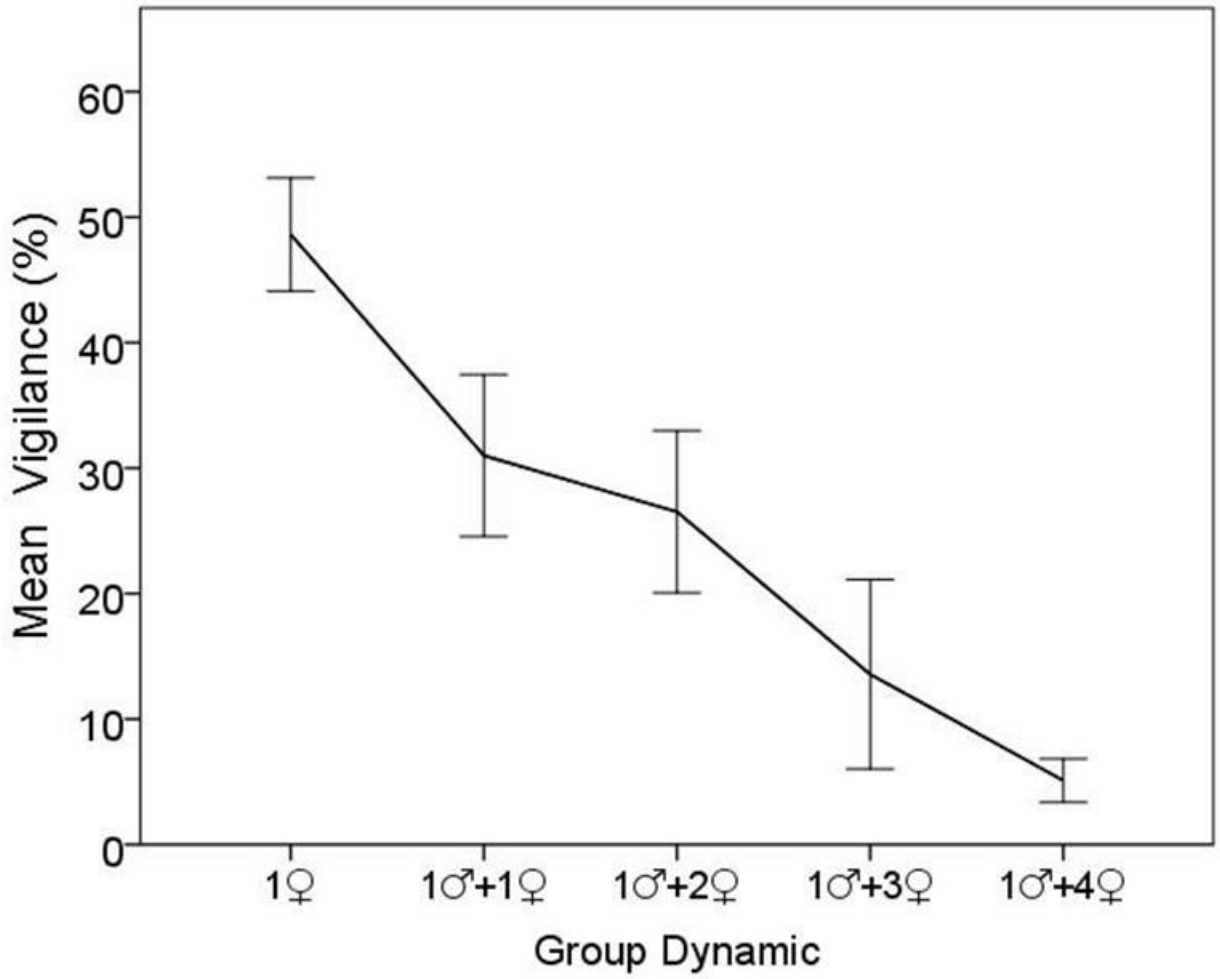


Figure 6.1. The mean percentage of time (± standard error) that a female spends being vigilant depending on group dynamic. There was no all-female group size above 1.

In contrast, individual females in larger groups engaged in higher rates of foraging (ANOVA: Polynomial Contrast: $F_{4,38} = 8.23$, $P < 0.001$, Figure 6.2).

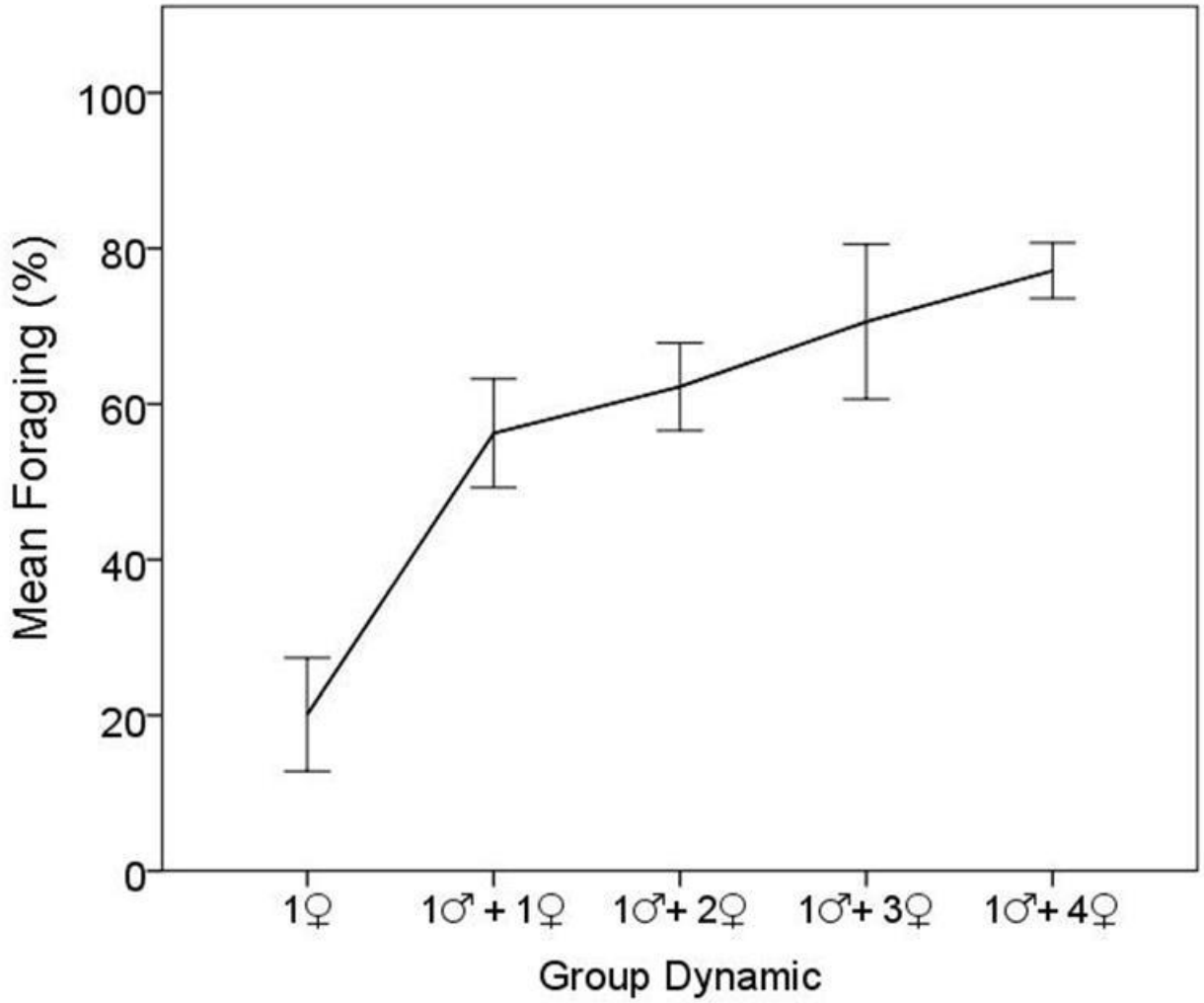


Figure 6.2. The mean percentage of time (± standard error) that a female spends foraging depending on group size. There was no all-females group size above 1.

6.3.2. Male behaviour in the wild

Solitary males, in this case indistinguishable between males with a territory and no harem and satellite males, were less vigilant ($\bar{x}$ = 36.94) than males which have a territory and a harem regardless of harem size ($\bar{x}$ = 70.20) (ANOVA: Territory: $F_{1,79}$ = 53.14, $P < 0.001$).

Males with larger harems exhibited increased *per capita* levels of vigilance than those with smaller harems (ANOVA: Polynomial Contrast: $F_{3,42}$ = 18.78, P = 0.001, Figure 6.3).

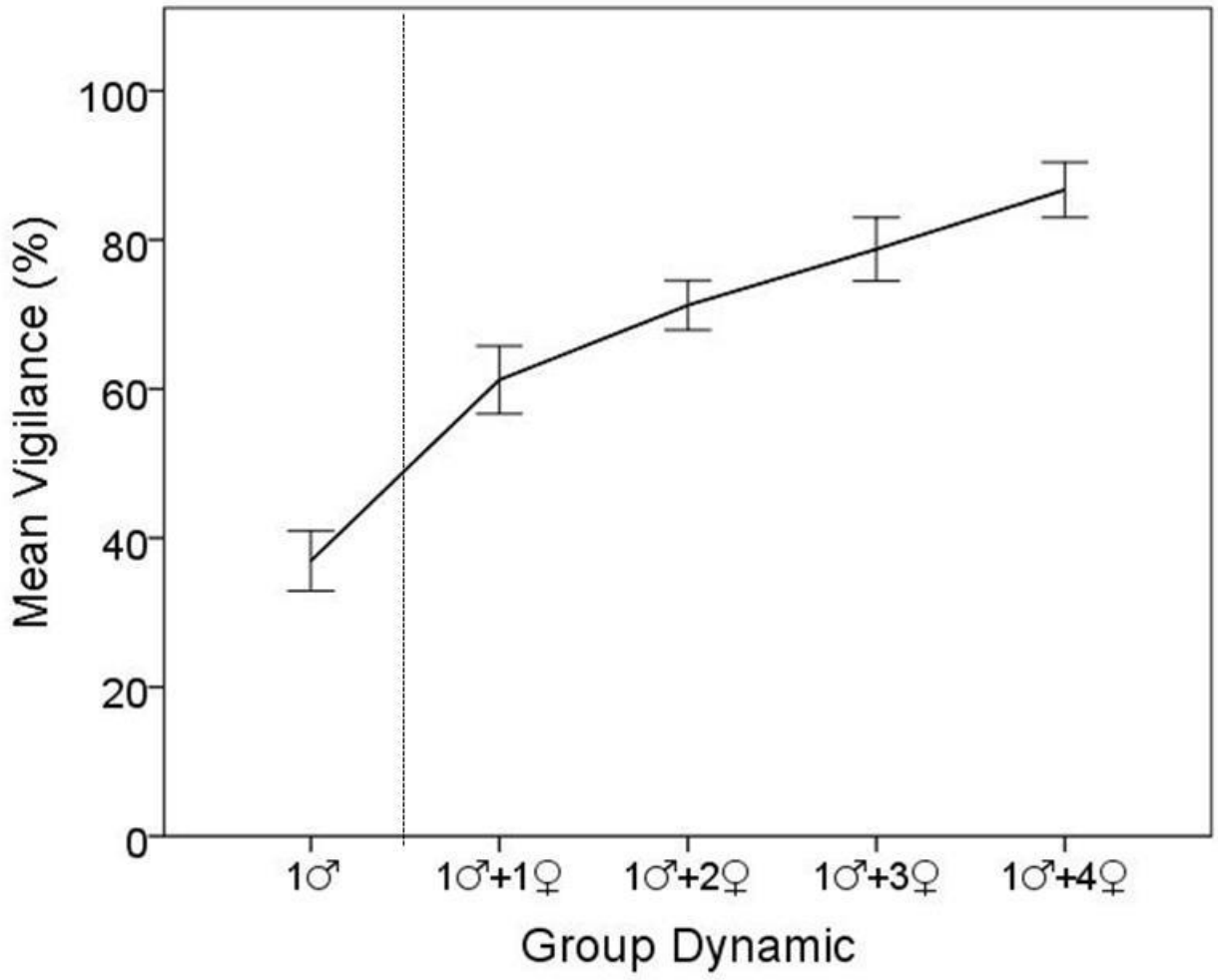


Figure 6.3. The mean percentage of time (± standard error) that a male spends being vigilant depending on group dynamic. Here 1♂ represents a solitary male that is either non territorial or territorial without a harem. There was no group with more than one male. There was no group with more than one male.

Solitary males, in this case indistinguishable between males with a territory and no harem and satellite males, foraged more ($\bar{x}$ = 10.95) than males which have a territory and a harem regardless of harem size ($\bar{x}$ = 27.01) (ANOVA: Territory: $F_{1,79}$ = 18.82, $P < 0.001$).

Males with larger harems spent less total time foraging than those in smaller groups (ANOVA: Polynomial Contrast: $F_{3,42}$ = -7.58, *P* = 0.029, Figure 4). This reduction in time was driven by a reduction in the number of foraging bouts that he engaged in, rather than the length of his foraging bouts, which did not differ across group sizes (ANOVA: $F_{3,36}$ = 0.393, *P* = 0.76).

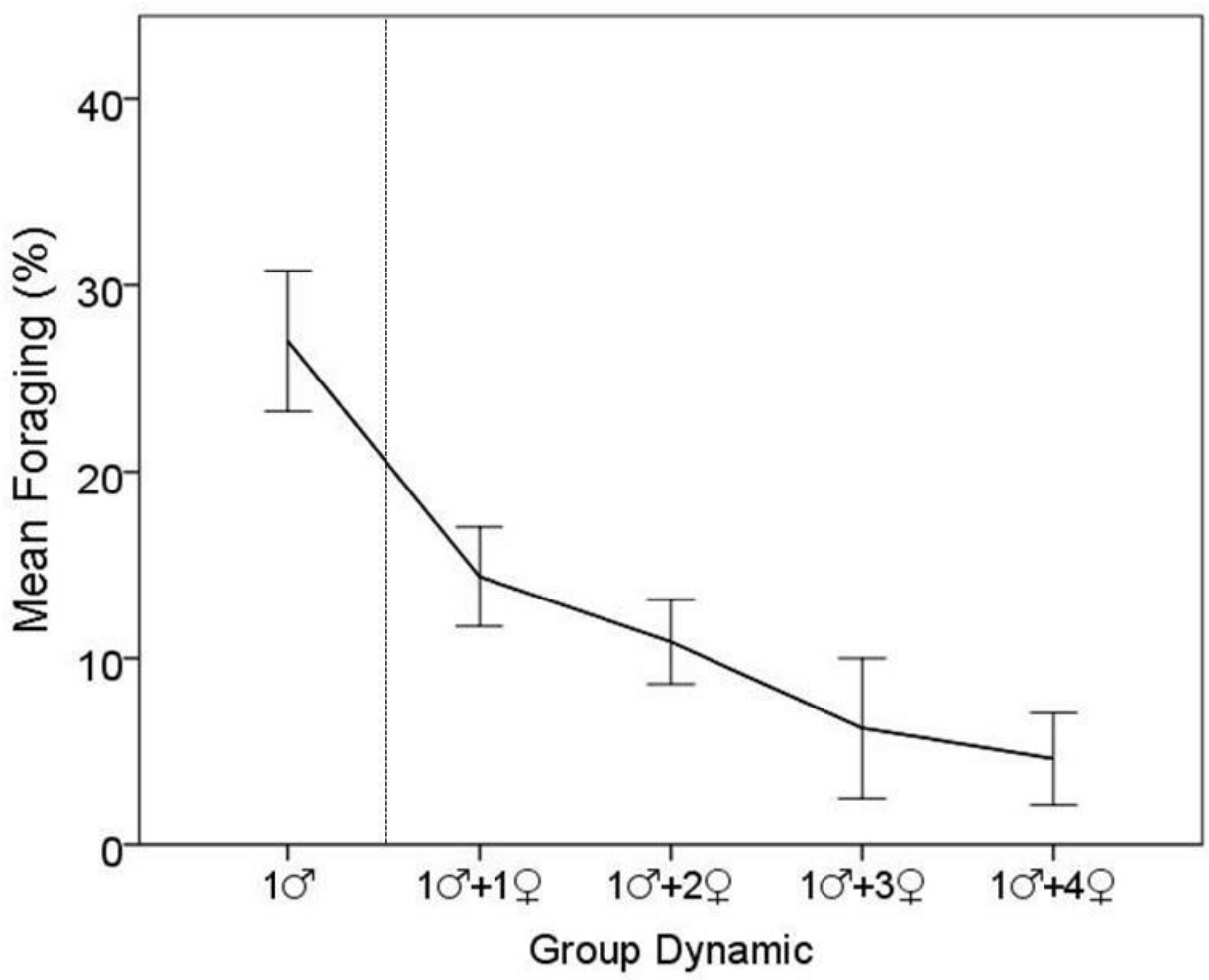


Figure 6.4. The mean percentage of time (± standard error) that a male spends foraging depending on group dynamic. Here 1♂ represents a solitary male that is either non territorial or territorial without a harem. There was no group with more than one male.

6.3.3. Repeatability

Due to many males being consistent in their harem sizes we were only able to conduct repeatability analysis on nine individuals, the test show that males were consistent in their vigilance behaviour when their harem size changed ($N = 9$, $r = 0.98$).

6.3.4. Aggressive interactions and incursions

There were no aggressive interactions between females, or between males and females. There was no incursion from neighbouring or satellite males.

6.3.5. Collective vigilance and optimal harem sizes

We calculated that a group comprising one male and two females would exhibit the highest collective vigilance compared to other group sizes and compositions, with coverage of 125.90% of the time, equating to at least one and a quarter individuals being vigilant at any moment (Figure 6.5). Deriving the maximum value of collective vigilance and its corresponding group size we found that the optimal vigilance for the population observed in this study with a male and a harem of 2.67 females.

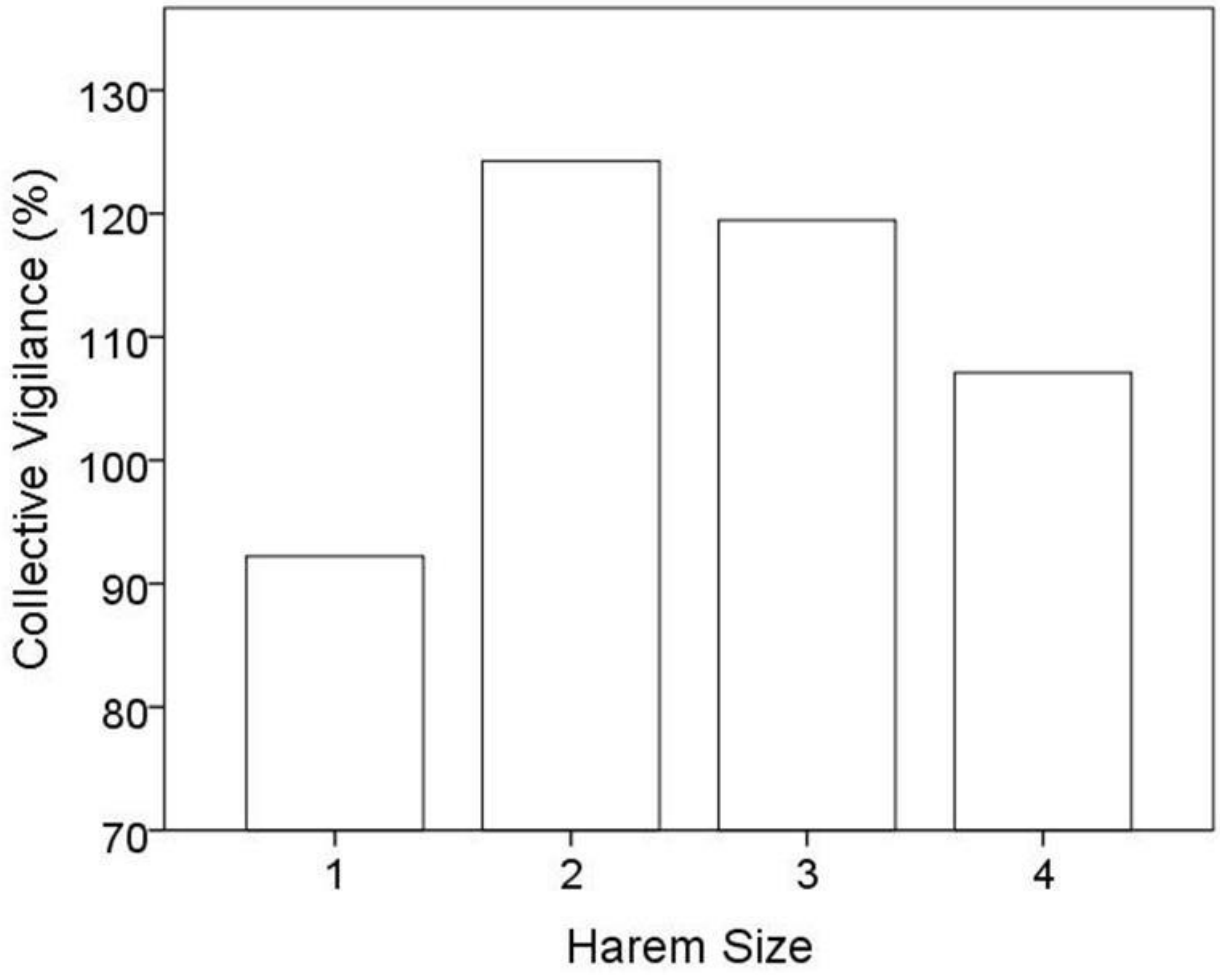


Figure 6.5. The combined group level vigilance depending on harem size.

The average harem size for this population of pheasants was a male with 2.07± 0.20 females closely matching the calculated optimal group size (Figure 6.6). Both the biologically realistic calculated optimal and observed harems comprised one male and two females. 43% of males did not hold a harem.

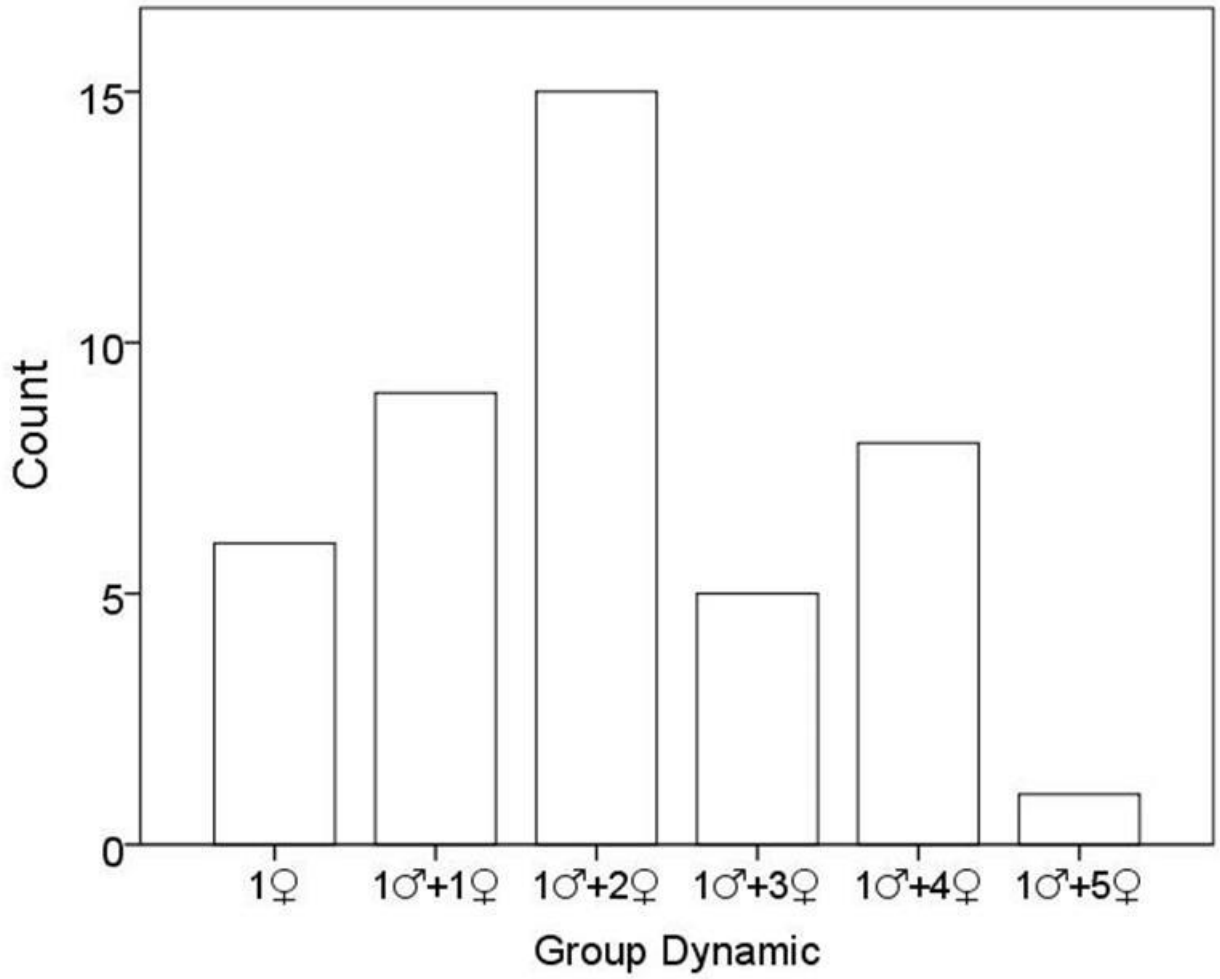


Figure 6.6. A histogram representing the counts of each group dynamic a female was found. There were no all-female groups.

6.4. DISCUSSION

Male pheasants are polygynous and do not offer parental care (Taber 1949), or territorial resources (von Schantz *et al.* 1989a; Göransson *et al.* 1990; Grahn, Göransson & von Schantz 1993c), yet we did not see large aggregations of females around a few popular males. Instead, we observed a much lower skew with around 57% of males attracted at least one female, with an average harem size of 2.07 females. Pheasants typically have an equal sex ratio during the breeding season (Grahn, Göransson & von Schantz 1993c); therefore we show that harem sizes in this population is not a function of random association. Harem sizes observed in this study are regularly documented in pheasants on other sites. This small harem size matches closely the size of harems in which we calculated there would be maximal group-level vigilance, suggesting that the factor determining harem size in this species is a desire to optimize vigilance coverage, whilst allowing females to increase their *per capita* foraging levels.

Females clearly benefit from joining larger groups, replacing their vigilance behaviour with increased time spent foraging. A solitary female joining a male reduces her vigilance level by 18%, allowing her to spend three times longer foraging. This three-fold increase in foraging was also observed in a previous study of pheasants (Ridley & Hill 1987), and similar benefits are observed in other mate guarding systems (Hannon & Martin 1992; Alberts, Altmann & Wilson 1996). As more females join the harem, individual female vigilance levels continued to decrease. The negative relationship between harem size and vigilance levels resulted in females in a group of four females (and their accompanying male) having an 25% reduction in vigilance percentage compared to a single female (and its accompanying male). This relationship was predicted to operate in pheasants by Ridley and Hill (1987) and has been observed in many group living animals adhering to the “detection effect” and “many eyes” hypotheses (Elgar 1989; Lima & Dill 1990; Roberts 1996). This reduction in vigilance is matched by an increase in time spent foraging. Females within a harem

of four females (and accompanying male) foraged for 21% longer than a female in a harem consisting of only her and her accompanying male. Increased *per capita* foraging is often observed in increased group sizes in birds (Sansom *et al.* 2008) and is beneficial for pre-laying females accumulating the fats and nutrients essential for egg production, incubation and brooding (Milne 1976; Christensen 2000). In pheasants this is described as a "digestive bottleneck" (Ridley & Hill 1987), whereby intake of large volume of low quality food does not equate to the energy uptake required for breeding therefore a male providing higher levels of vigilance will reduce undue energy expenditure as a result of harassment from other males. Flying from these disturbances can be up to 15 times more energetic than basal metabolism, and such depletion cannot be recouped by foraging, purely from the depletion of energy reserves (Bautista, Tinbergen & Kacelnik 2001). This is especially important for hen pheasants as they can lose up to 40% of their body mass during the reproductive season (Robertson 1994). This loss of condition is considered to be one of the key factors that cause high mortality during the spring (Hoodless *et al.* 1999). We observed no aggressive interactions between females unlike in resource based harem polygyny systems where females are vigilant, territorial and aggressive to try and deter recruitment (e.g. redwing blackbirds (*Agelaius phoeniceus*) (Hurly & Robertson 1984; Hurly & Robertson 1985). This suggests that in pheasants there was no intra-harem female-female competition or interference for resources, and those females did not use coercion to influence harem size. A small time period used for observations could mean that we missed these interactions, but there is no evidence of coercion in other pheasant populations that I am aware off.

Males show the opposite behavioural shifts to females. A solitary male, for the purpose of this study could be a territorial male without a harem or a satellite male, will spend 25% less time being vigilant than a male with a single female. For territorial males, as the harem size increases, male vigilance also increases. Males with 4 females are 25% more vigilant than a male with only a single female in his harem. This

suggests that male vigilance may be directed towards competing males, as well as predators, and so is analogous with other mate-guarding systems, e.g. baboons (*Papio Anubis*) (Packer 1979) and ptarmigan (*Lagopus lagopus alleni*) (Bergerud & Mossop 1984; Hannon & Martin 1992)**.** Male pheasants will detect and actively chase harassing males from the harem (Hill & Robertson 1988j). Males also identify a disproportionate number of predators (Bergerud & Mossop 1984). Therefore, high vigilance brings a male two forms of benefit; 1) increasing his reproductive success by protecting the harem from predators (Bergerud & Mossop 1984); and 2) maximising his paternity by minimising extra pair copulations (Beecher & Beecher 1979; Birkhead 1979). The cost of high vigilance is a corresponding decrease in time spent foraging. A male with a single female had half the foraging time than a solitary male. Reduction in foraging time of mate guarding males can lead to rapid loss of condition (Alberts, Altmann & Wilson 1996). Costs of reduced foraging continued to rise as harem size increased. Males with a four female harem will forage 68% less than a male with only a single female in his harem. This cost of foraging is not a result of smaller bout lengths but simply the amount of foraging bouts available for a male. Therefore, whilst males attracting females to their harems have access to more mates and increasing reproductive success (Holm 1973), and more general group augmentation benefits (Altmann, Wagner & Lenington 1977; Wittenberger 1979), males exhibit clear costs from increasing harem size through reduced foraging levels. Despite this cost of allowing females to join a harem, males did not exhibit any aggression towards the females and so we assume that coercion is not a factor used by males to maintain harem size.

The modal size of harems that we observed matched closely the harem size in which combined vigilance was highest, suggesting that harem size is primarily influenced by a desire by the constituent members to maximise group-level vigilance. Both the predicted value and the observed values were greater than if there was an equal sex ratio and each female acted randomly. Although our modelled harem size was 2.67 and the actual mean harem size was 2.07 females, we feel that the modelled

value would be even closer to this value if we included the vigilance of solitary individuals in the model. However, we were unable to distinguish between male with a territory and no harem and those which are satellite males. At another study site, harems comprised two females or fewer Ridley and Hill (1987).

We calculated that at our study site, harems comprising one male plus two females would exhibit the highest group-level vigilance. Group sizes larger than this showed a reduction in group-level vigilance. This continued reduction is likely because the male is unable to match the declining vigilance levels of the females joining him, whilst the females continue to cut their own levels of vigilance on joining a group. This continued decline in vigilance by females may be due to two factors. First, additional females may engage in a 'race to the bottom' cutting their own vigilance in an effort to avoid being exploited by the other group members. Alternatively, additional females introduce competition or disruption in foraging behaviour so that all females have to invest more time in foraging in order to maintain nutritional intake with a corresponding decline in their vigilance behaviour. Our observations cannot separate these alternative explanations. Individual optimal vigilance and foraging levels are likely to vary with predator numbers and forage quality, and this could explain why some pheasant populations have different average harem sizes (Robertson 1986). Reasons why we see group sizes differing from the modal harem size could be related to non-vigilance based group augmentation benefits such as information acquisition and transfer (Clark & Mangel 1984; Giraldeau & Dubois 2008) or the costs of searching for mates (Alatalo, Carlson & Lundberg 1988).

We emphasise that this is a purely correlative study and although we found evidence of repeatability, and therefore males are consistent with their vigilance behaviour across harem sizes, this was only based on a relatively small sample of individuals (n=9) that were identified as having different harem sizes on different occasions. The lack of variability in harem sizes could be because the study was

conducted close to the onset of the females laying eggs and therefore the females may have made their choice and therefore were not inclined to move between males. The result suggests that attraction is a factor in harem dynamics and those females could be using vigilance levels in mate choice. This consistency also indicates that males do not intrinsically become more vigilant as harem size increases. This result is surprising as studies on mate choice in pheasants indicate that female use only morphological cues (Ridley & Hill 1987; von Schantz *et al.* 1989d; Göransson *et al.* 1990; Hillgarth 1990; Grahn, Göransson & von Schantz 1993c; Mateos 1998)**.** These studies are often conducted in captivity, hence, in the wild; with the added stress of predation and harassment, the hens may also use behavioural cues in mate choice. Vigilance behaviour of grey partridge (*Perdix perdix*) is the only behavioural trait used in mate choice (Dahlgren 1990). A more controlled approach is needed. One way is to use of a marked population to observe birds multiple times with natural variations in harem size. Another method would be to use bird caught as a part of a restocking programme (Hill & Robertson 1988j) and artificially manipulate the harem size.

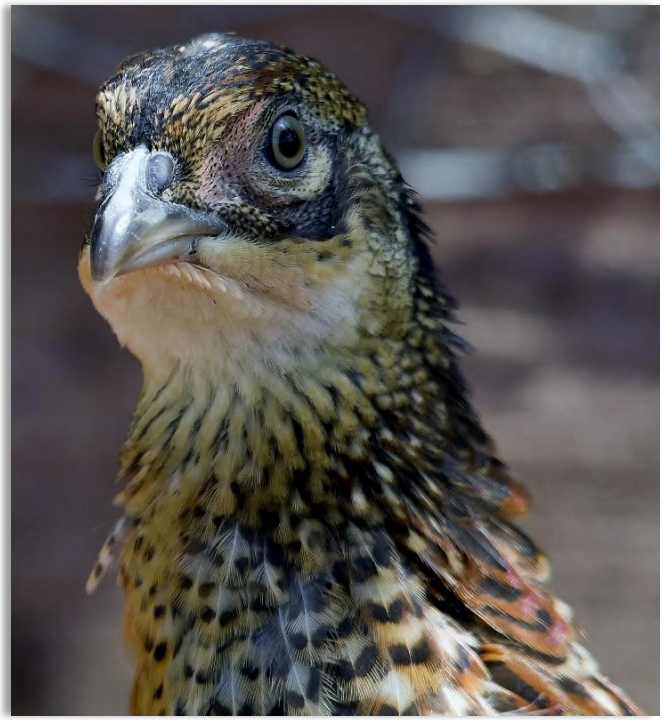
For group living animals it is typical for there to be no detriment in collective vigilance as group size increases and individual vigilance decreases (McNamara & Houston 1992) and within these models it is competition for resources that limits group sizes (Clark & Mangel 1986; Wrangham, Gittleman & Chapman 1993). However, these models are often attributed to non-breeding animals. We suggest that both male and female motivation and behaviour should be incorporated when exploring optimal group size models for animals that adopt harem defence polygyny mating systems. The resolution of harem size does not appear to be determined by coercion and violence by either sex. Instead, harem size seems to be a product of balancing costs and benefits of vigilance and foraging in a dynamic system. Differences in harem size around a male is not influenced by the territory and the food abundance as harem size was not influenced by food availability (Hoodless *et al.* 1999), territory size and habitat structure (Ridley & Hill 1987) and therefore male quality is more important than territory quality in

pheasants (Ridley & Hill 1987; Göransson *et al.* 1990; Grahn, Göransson & von Schantz 1993a; Grahn, Göransson & von Schantz 1993c). Although males lack a resource, females utilise male vigilance behaviour to benefit in terms of increased foraging time, protection from predators and protection from harassing males.

The linear relationship observed between vigilance levels of the male and harem size, and the costs associated with reduced foraging indicates that at low harem sizes the males can supplement the reduced vigilance of females to maintain high group-level vigilance. However, males are unable to compensate with the necessary vigilance to maintain group-level vigilance as harem size increases and individual contributions by females decreases. Therefore the harem size is strongly influenced by vigilance behaviour of constituent members. Despite a shared interest in increasing harem sizes, their optimal size is influenced by trade-offs in individual vigilance behaviour, resulting in relatively small harems, perhaps leading to females associating with otherwise less preferred males, and males being surrounded by fewer females that he could mate with. Consequently, mating skew may be constrained by vigilance demands, and so shaped by the local predatory environment.

Chapter Seven

General discussion



7.1. INTRODUCTION

In animal conservation there is a concerted effort to improve the success of translocation programmes (Armstrong & Seddon 2008), particularly those that use captive propagation (Griffith *et al.* 1989; Wolf *et al.* 1996). After release into the wild, animals reared in captivity often exhibit high mortality (Kleiman 1989; Snyder *et al.* 1996; Fischer & Lindenmayer 2000) and dispersal (Stamps & Swaisgood 2007; Armstrong *et al.* 2013). Deaths and losses from controlled areas mean that excessive animals need to be released at a site in order to achieve desired established population outcomes, and this introduces environmental, ethical and financial costs to the programmes. This thesis has proposed two simple approaches by which these costs can be reduced and thus improve the efficiency of the release programme.

The first area is that of manipulating the captive rearing conditions experienced early in life by animals destined for release into the wild, in order to assist their development to make them better suited to the natural environment post release. I used a model study system to explore questions usually restricted to rare or endangered species. I used the high sample sizes, replicable conditions, individual marking and robustness of the pheasant and the pheasant rearing system to allow the collection of morphometrics and behavioural tests whilst in captivity and I combined this with focused post release monitoring, retrieval and post mortem analyses to conduct a holistic approach to examine general patterns of behaviour and development. I combined research already conducted in social learning, reintroduction biology and captive rearing techniques to provide a cost effective and non-labour intensive manipulation to a pheasant rearing system. **Chapter two** explored how the provision of a more naturalistic diet, precluded in current rearing methods, influenced survival of the animal after release. Using behavioural tests in captivity, observations in the wild and detailed post mortem analysis I was able to determine what mechanisms may have caused the birds reared with more naturalistic diet to survive better in the wild. **Chapter**

three explored how the provision of a more complex environment, in the form of elevated perches, influence survival after release. Using morphological measurements taken prior to release, observing birds in the wild and detailed post mortem analysis I was able to suggest possible mechanisms for why birds reared in barren or simple environments had higher likelihood of being predated. To complement the work, **Chapter four** asked if these manipulations had welfare consequences on animals prior to release, furthering the holistic approach of the project.

The second area drew information from the field of personality and **Chapter five** looked at how individual behavioural differences can influence survival and dispersal of animals released in high numbers. By assaying individuals prior to release, I could better understand their likely fates and movements. I found birds that were designated as being shy and less social were more likely to die of natural causes or disperse from the release site completely.

Chapter six was more fundamental in nature, looking at what restricts harem sizes in the wild and ultimately reproductive success of male pheasants. I found that individual male vigilance behaviour plays an important role in harem sizes.

This discussion summarises and examines the implications of the findings and is separated into three sections: 1) implications specifically to the pheasant industry; 2) broader implications for the field of reintroduction biology; and 3) future directions for the work. In these sections I will look at benefits to the fields and influences of personality. I will finally defend why a holistic approach is essential for reintroduction biology.

7.2. IMPLICATIONS FOR THE PHEASANT REARING AND GAME INDUSTRY

7.2.1. Manipulating the rearing environment

Over 40 million galliformes are reared and released each year in the UK for the shooting industry, predominantly originating in similar, highly intensive, barren, motherless and predictable rearing facilities. Reared pheasants and partridges that are released into the wild suffer from many developmental deficiencies (Robertson, Wise & Blake 1993; Draycott *et al.* 1998; Hoodless *et al.* 1999; Buner & Schaub 2008; Rantanen *et al.* 2010), leading to high mortality prior to the shooting season (Robertson 1988; Brittas *et al.* 1992; Rymešová, Tomášek & Šálek 2013) and poor reproductive success for those who survive the shooting season (Hill & Robertson 1988a; Sage *et al.* 2003; Buner, Browne & Aebischer 2011). Unfortunately there are very few studies looking to influence galliform rearing conditions with the aim of improving survival after release. Homberger *et al.* (2014) used a relatively simple manipulation to the feeding regime to look at how it impacted survival, showing that the provision of an unpredictable food source can aid survival by increasing coping mechanisms for stress. Some studies have shown that rearing with parents or surrogate parents increased chick survival into adulthood (Buner & Schaub 2008; Bagliacca *et al.* 2010; Ferretti *et al.* 2012). The survival of these enriched/parented birds is impressive, and I considered the use of surrogate chicken hens to raise pheasant chicks but the labour and the financial costs involved in this method would mean that intensive game rearing facilities might not be able or keen to return to this method of rearing on an industrial scale. This is because under a hen a maximum of 15 chicks can be reared (Coles 1975), and so to accommodate this in the UK a minimum of 2.2 million surrogate chicken hens will be required for rearing, add to this a surplus of bantams as only broody hens will become surrogates. Whereas using artificial rearing environments as many as 1000 birds can be reared under a single heat lamp. Therefore there is obvious criterion that need to be reached in order for the game industry to adopt a new rearing strategy, therefore manipulations must: 1) influence the development of important survival skills and that

these characteristics improve survival of the released individual without losing trade; 2) be cheap to employ in terms of finance and labour. In order to garner popular support and indeed legal sanction, the new methods should also offer 3) an environmental benefit; 4) and ethical benefits.

7.2.1.1. Can rearing manipulations influence post release behaviour and survival

Conditions experienced during early development can affect behavioural, physiological and cognitive development (Lindström 1999; West-Eberhard 2003; Buchanan, Grindstaff & Pravosudov 2013); this was no different in this study. In **Chapter two**, compared to control birds, birds reared with a more naturalistic diet had better foraging efficiency, were more vigilant, had a more diverse post-release diet and a gut system more adaptive to a high energy food intake. Birds reared with a naturalistic diet, on average were five times more likely to be alive after one year in the wild than birds reared in the control conditions.

In **Chapter three**, compared to birds reared in barren environments, birds reared with access to perches had a higher propensity to roost as adults were physiologically more adapted to reaching elevated perches and to maintain roosting for an extended period of time. In addition birds reared with perches had better working spatial memory, which could aid an individual's ability to remember feeding, roosting and refuge sites (Bauchot *et al.* 1977; Gill & Wolf 1977; Janmaat, Byrne & Zuberbühler 2006). Birds reared with early access to perches were seven times less likely to die of natural causes than birds reared in controlled conditions.

It was important to note here that in both **Chapter two** and **Chapter three** I found no difference in the number of pheasants being shot across rearing treatment, therefore the manipulations did not have a detrimental effect on the focus of the shooting industry, that is numbers of birds shot.

7.2.1.2. Environmental benefits

Although the shooting industry provides some environmental benefits in terms of habitat management and supplementary feeding, the release of pheasants can impact on the release ecosystem (Clarke & Robertson 1993; Sage, Ludolf & Robertson 2005; Sage *et al.* 2009). The release ecosystem would benefit from the release of fewer birds at lower densities as it would reduce disease burdens for both the released individuals and the wild population (Gortázar *et al.* 2006) and enhance biodiversity or survival of key indicator species (Sage, Ludolf & Robertson 2005; Draycott, Hoodless & Sage 2008a; Sage *et al.* 2009; Callegari *et al.* 2014). The survival benefits observed in this study could facilitate this, with the opportunity for fewer birds to be released, each with a higher chance of survival, yet still supplying an economically viable shootable surplus of birds for the shooting industry.

I have used a number of sources to determine the mortality of birds during the first year after release into the wild. The reason for this is that no studies looked at the fate of birds for the full year. For the fate of birds between release and the end of the shooting season I refer to Turner (2004), specifically I am interested in the 32% of birds predated prior to the end of the shooting season. For the fate of birds between the end of the shooting season and the end of the breeding season I refer to Hoodless *et al.* (1999), specifically interested in the 71% mortality of pheasants during this period (See Figure 1.1). From these figures I can determine what my results mean on the scale of pheasants released in the UK by using 35 million pheasants released each year as a benchmark (PACEC 2008).

Using current methods we expect to see a 9.23% of the released population dying between the end of the shooting season to the end of the breeding season. Using actual survival benefits from this study, then I would expect that if all birds released in the UK were reared with access to naturalistic diet the number of birds dying after the shooting season would be 7.38%. This equates to 2.58 million more

birds surviving this period. Using conservative estimates, as one fifth of the benefits obtained in the study then I would expect to see 1.92 million more birds surviving to the end of the breeding season.

Using current methods we would expect to see 32% of the released population dying from predation before the end of the shooting season. Using actual benefits from this study, then I would expect that if all birds in the UK were reared with access to perches, the number of birds dying from predation before the end of the shooting season would be 27.43%. This equates to 9.6 million more birds surviving this period. Using conservative estimates I would expect to see 1.92 million more birds surviving to the end of the breeding season.

7.2.1.3. Financial benefits

To establish the economic benefits associated with the rearing conditions adopted in this thesis it is important to look at two aspects of the pheasant industry. The first is the short term costs associated with adopting my rearing methods. The second is to look at the long term benefits to the landowner and the game industry as a whole (for summary see table 7.2).

In 2013, for the six week rearing period I provided 450 pheasants with mealworms, this calculated as 12.27p *per capita*, and took fractions slower to feed the birds than using the traditional methods of feeding. The normal cost to buy a bird at six weeks old is £3.65 (SmithsGore & GWCT 2014), if I use this value as a conservative estimate of rearing costs (as costs would be less to account for profit for the game rearer), then to rear birds with mealworms for the six week period will cost £3.82, an increase of 3.6%). Unlike manipulation of diet where there is an annual cost associated with the supplementary feed, the provision of perches would incur an initial outlay and subsequent years the cost would be negligible. I used artificial perches in the form of conduit piping, costing £0.42 per meter. Current minimum welfare recommendations for

intensively reared chickens suggest a perching distance of 0.15m per bird (CEC 1999; Appleby 2003). This equated to an extra £0.06 per bird for the first year of the study, therefore increasing the rearing cost to £3.72, an increase of 1.9%.

Although the cost to rear a bird is around £3.65, the release and maintenance of a pheasant on a shooting estate has greater costs than this. Costs also include feed, vet bills, advice from consultants, keeper wages, insurance, management costs, vehicle costs, and more. Combining these costs equates to £13.76 for every bird released onto the estate (SmithsGore & GWCT 2014). The long term economic benefits of adopting one of the rearing strategies suggested in either **Chapter two** or **Chapter three** is based on the number of fewer birds required to be released each year to obtain the same shooting and same survival as current rearing methods. Therefore, using the actual survival benefits observed with the provision of a naturalistic diet (**Chapter two**), releasing 2.58 million fewer birds to obtain the same number of birds surviving the first year, the saving to the UK game industry would be £34.25 million a year. With the conservative estimate, releasing 0.52 million fewer birds would save the UK game industry £7.05 million each year (table 7.1).

If the entire UK game industry adopted the habitat complexity adopted in **Chapter three**, then after the initial outlay of £1.62 million on equipment, using the actual benefits I would expect to see a first year saving of £130.48 million for the UK game industry, subsequent years would see more profit of £132.10 million. At the more conservative estimates of survival, after an initial outlay of £2.22 million, subsequent years would see savings of £26.41 million (table 7.1). The use of natural perches, in the form of hazel wands, can act as a cheap alternative. These would be free with landowner's permission except for a minimal labour costs. However, conduit piping may be better in the long-term as it can be fixed in place and easily cleaned.

Having more birds surviving the winter means that there are more birds available for reproduction, and therefore will start to supplement the natural stock. With this supplementation into the wild population it may mean that even fewer birds will be required to be released in subsequent years.

a) Birds fed with naturalistic diet	*Actual benefit*	*Conservative benefit*
Numbers released each year	35.00	35.00
Cost to keep a bird for shooting purposes	13.76	13.76
Cost of current regime to the UK shooting industry	481.60	481.60
How many fewer birds required to be released	2.58	0.52
Cost of adopting our method UK wide (projected)	446.04	474.49
Cost of adding mealworms per capita	0.12	0.12
Cost of rearing all birds on mealworms	0.32	0.06
Net financial benefit	35.24	7.05

b) Bird reared with access to perches	*Actual benefit*	*Conservative benefit*
Numbers released each year	35.00	35.00
Cost to keep a bird for shooting purposes	13.76	13.76
Cost of current regime to the UK gaming community	481.60	481.60
Number of fewer birds required to be released	9.60	1.92
Cost of perching per capita	0.06	0.06
Fist year outlay	1.62	2.22
Financial benefit	132.096	26.4192

Table 7.1: Representing the projected benefits based on actual and conservative benefits for birds reared with: a) more naturalistic diet; and b) early access to perches.

7.2.1.4. Ethical benefits

Releasing pheasants which have the behavioural, physiological and cognitive ability to survive improves the ethical dimension of the release programme. In addition, this survival allows for fewer birds to be reared and released each year contributing to a more general ethical benefit.

It is well established that the best way to improve the development of important survival skills is to replicate conditions experienced in the wild. However, natural conditions will also promote fear, stress and discomfort, factors that captive managers want to avoid (Rabin 2003). This risk of compromised welfare by introducing a more naturalistic and perhaps harsh rearing environment could be one of the reasons why we have seen little advancement in rearing conditions to promote survival in intensive

rearing environments with the intention for release. I however found that the addition of stimuli in the form of enriched diets or additional perching opportunities to promote development of survival skills does not have to compromise welfare; in fact I found that the additions improved pre-release welfare. In **Chapter four**, I assessed the welfare implications of enriched environments and found that having access to perches caused a reduction in aggression and access to naturalistic diet increased psychological wellbeing as indicated by increased rates of preening. Although there is code of practice for the welfare of gamebirds reared for sporting purposes (DEFRA 2009), which tries to ensure that gamebird needs are met, detailing the provision of water, appropriate diet, space, avoidance of disease and freedom to perform natural behaviours, pheasants and partridges likely suffer from high levels of aggression (Prieto *et al.* 2012), to such an extent that "bits" and drugs are used to reduce its impact (Butler & Davis 2010). However, these management interventions do not identify the root causes of the poor welfare (Nicol *et al.* 2013). The reduction in aggression as a result of the provision of perches could be the first step to rid the system of management devices to restrict the damage of pecking. If the addition of perches reduces aggression to such as extent that mechanical devices are not required then it would benefit the industry in a number of ways: 1) application and removal of 'bits' requires catching the birds at three-weeks old for application and then again at six-weeks old for removal, therefore adding unnecessary stress to the population; 2) although 'bitting' provides a useful tool in halving the number of bird-on-bird pecking, there are still welfare issues of wearing the devices such as increased head shaking, scratching, inflammation of the nostril and bill malformation (Butler & Davis 2010); 3) these bits are unnatural devices which can disrupt the field of view which inhibits learning and behaviour (Ferretti *et al.* 2012); and 4) financially, 'bits' retail at around £13 for 1000 birds, equating to around £455000 year spent in the UK annually. In addition they take time to fit, to catch and de-bit 1000 birds took two men two days (GWCT 1994). Using the minimum wage as a standard, I calculate that it could cost £910000 in labour costs to attach 'bits' to all pheasants reared in the UK

each year. Therefore I estimate that bitting in total costs ~£1.4 million every year. I suggest that adding perches could substantially reduce this cost. However, the results from my study may not scale to industrial levels. I used a low population size (n=30) and a stocking density (~20 bird per meter$^{2)}$ about half that seen in a typical commercial rearing setup (~43 bird per meter^2) (Farm Animal Welfare Council 2008). Aggression generally increases with stocking density (Nicol *et al.* 1999; Zimmerman *et al.* 2006), but not always with increased group size (Hughes *et al.* 1997), there is a need to test these enriched conditions on higher populations sizes to find its effectiveness in relation to normal populations (see 7.5.2: future direction).

My provision of a more natural diet resulted in birds which appeared to be in a state of improved psychological welfare. This reduction of stress plays an important role in release programmes: 1) less stressed animals prior to release often make a better transition to life in the wild (Teixeira *et al.* 2007); 2) stress can influence behavioural, cognitive and physiological development (McEwen 1999; Cam, Monnat & Hines 2003; McEwen 2008), making stress prior to release important in systems that require learning of important survival skills; and 3) wildlife managers are morally and often legally obliged to maintain a high level of welfare, and therefore it is important to promote efforts to improve welfare, particular in systems where large numbers are reared for release.

The code of practice (DEFRA 2009) was welcomed but lacks detailed research on which precise recommendations might be based (Record 2010). This is because little work has been conducted on the welfare of game birds, a result of minimal official surveillance or monitoring of gamebird premises (Hunting 2008). Although there is one article describing how visual barriers can influence welfare in adult breeding facilities (Deeming, Hodges & Cooper 2011), there is no work that I am aware of looking at methods to increase the welfare of pheasants reared for release. This is the complete opposite in intensively reared broiler hens, where in recent years there has been an

explosion in the literature trying to better welfare. Therefore, this study is one of the first to look at how cheap and non-labour intensive manipulations to the current system, with the primary aim of improving the development of traits that aid survival, can promote welfare. I hope that the work stimulates other such studies on intensively reared animals for release.

7.2.1.5. Dangers of misuse

One of the biggest dangers with this study is that the shooting industry utilises the increased survival without reducing the numbers released. This may cause both local and national ecological damage. For instance if birds were reared with naturalistic diet, I would expect 2.58 million more birds in the UK countryside in the spring. This could have a devastating effect on the landscape, particular if game-keepers ceased supplementary feeding during the spring months as is unfortunately very common at present (Draycott *et al.* 1998). If the game-industry adopts rearing with perches, it may find increased survival prior to the end of the shooting season, but then when the season is over and with the cessation of supplementary feed, these birds will starve or compete for sparse natural resources with native wildlife. Therefore it is important to educate the shooting industry that these rearing strategies will only have ethical and environmental benefits if they release fewer birds.

7.2.2. Impact of personality

Chapter five highlighted how inherent individual differences across suites of behaviour, captured by the paradigm of personality, can predict individual fate and post-release dispersal occurring in a translocation programme. Personality is an expanding field of biology (Van Oers *et al.* 2005) and becoming more important in applied biology (McDougall *et al.* 2006; Réale *et al.* 2007).

7.2.2.1. Can individual personality predict their post release fate and behaviour?

I found that releasing high numbers of birds caused birds that were shy and less social to either: 1) disperse from managed areas which are abundant in food, water, shelter and medication, which makes them more susceptible to dying from natural causes; and 2) disperse from the release site entirely, reducing the amount of birds available to breed the following year. The results were interesting because generally bold individuals that disperse further (Fraser *et al.* 2001; Bremner-Harrison, Prodohl & Elwood 2004) and have higher rates of mortality (Réale *et al.* 2007; Smith & Blumstein 2008). I attribute the results found in **Chapter five** to the numbers involved in the release being far greater than the numbers of pheasants which appear naturally in the wild, making the release site inhospitable for the shy and less social birds.

7.2.2.2. How would understanding individual personality prior to release assist the release of game?

Dispersal from the release site, and death within the release site reduced the number of animals remaining in the founder population, and therefore reduced the likelihood of creating a self-sustaining population (Armstrong & Seddon 2008; Mihoub *et al.* 2011; Armstrong *et al.* 2013). Specifically for game-release there is a financial benefit for the landowner to keep released stock alive and on the release site, meaning that there are more birds available to shoot and after the shooting season, a larger population remains to breed. Therefore by understanding how personality affects post release fate and dispersal, identifying solutions to mitigate these effects is possible. For instance, now knowing that shy and less social birds are more vulnerable to predation and had a higher likelihood of dispersing from the release site, potential changes to release methods can be suggested. Sociability is density dependent (Cote & Clobert 2007) and shyer birds are often ousted from desirable areas (Cote *et al.* 2010). One way to stop this is to create a release environment that is amiable to all [or can retain all] personality types, this can be achieved by: 1) reducing the density of birds released, therefore making it more amenable to less social birds; or 2) create an

environment that restricts monopolisation of resources such as feed, water and shelter stations. This can include alterations to feeding regimes such as moving from a hopper based system to scatter feeding; scatter feeding involves spreading food over a wide area resulting in less monopolisation of a single clumped resource. From a shooting industry perspective, scatter feeding is more time consuming, and likely more wasteful with feed being lost in the ground or eaten by unintended animals, but it may offer greater environmental benefits, feeding non-target species, as well as benefiting the shooting industry by retaining birds in the release area more effectively.

7.2.2.3. Consequences of differential selection on personality types

The current methods of release followed by driven shooting typical in the UK suggests that there will be an over representation of shy personality types at the end of the season (Madden & Whiteside 2014). Personality is heritable (e.g. Dingemanse *et al.* 2002; van Oers *et al.* 2004) therefore artificially selecting for a personality type will result in a skew in subsequent generations and can impact the evolutionary trajectory of the programme (Allendorf *et al.* 2008). Over representation of particular personality traits is counter-productive for the establishment of a sustainable population as variability will better prepare a population to cope with fluctuating environmental conditions (Stamps & Swaisgood 2007; Watters & Meehan 2007). One way to counteract this is to reduce the number of bold birds shot each year therefore leaving a more representative sample in the population for reproduction. This could be achieved in three ways: 1) test the personality of birds prior to release and artificially select the birds to suit the release as suggested by Watters, Lema and Nevitt (2003); 2) use multiple releases at different times of year, e.g. release shy and less social birds in low numbers during the early hunting season, and then supplement with bolder and more social birds later in the year; and 3) create a release site that allows birds from all personality loadings to remain during the shooting season (see section 7.2.2.2). The first two solutions require ‘personality testing’ vast numbers of birds and hence are unlikely to be commercial acceptable (see below). Therefore, there should be focus on

the third option. By catering for all personality I expect that there will be an equal representation of personality types in each flush, meaning that equal proportions of birds will be shot, and a more representative sample will remain in the population to breed from.

7.2.2.4. Can assaying individual personality in the game rearing industry be effective

Assaying individuals prior to release and selectively choosing release composites based on personality have been suggested as a way of influencing the success of release programmes (Watters & Meehan 2007). This may work in studies that have low release numbers, for example only 59 swift fox were released in Bremner-Harrison, Prodohl and Elwood (2004) study. However in systems that require high release numbers, or have short periods of time in captivity, this may not feasible. In these situations the field of personality should not be completely discarded. It is important to understand how personality can influence survival, dispersal and future development, but assaying animals prior to release may not be the answer. I believe that studies like that in **Chapter five** are essential as it provides evidence that then allows for future ways to accommodate personality type through *in situ* management.

7.2.3. Introduction to reproduction

The majority of the thesis concentrates on mortality and dispersal, both factors which influence the number of birds remaining on a release site. However, pheasants which do survive suffer often suffer from poor reproductive success. There is work looking at pheasant mating system (Ridley 1983; Ridley & Hill 1987), however there have been no studies looking to determine what behavioural mechanisms may influence reproductive success (Anderson 1964; Brittas *et al.* 1992; Sage *et al.* 2003). **Chapter six** found that harem size is restricted by vigilance levels in the male. Understanding this allows for the shooting industry to focus future research, perhaps concentrating on factors that may influence behaviour during the breeding season and

therefore allowing the released birds to compete with wild conspecifics (See 7.4.4). This work aims to provide the background to future work trying to promote the development of characteristics that will allow for better reproductive success.

7.3. General implications for reintroduction biology

It is understandable that there is a dichotomy between management and research. Wildlife managers aim to manipulate rearing systems to promote establishment and persistence in critical conservation situations, whereas research scientists frequently aim to discover the mechanisms behind the system (Macnab 1983). As a result, reintroduction biologists have a number of obstacles. Current work on rare and endangered species has restricted sample sizes to allow for controlled and replicable conditions, is often unfocussed with poor monitoring (Armstrong & Seddon 2008), insufficient project duration (Beck *et al.* 1994) and a reluctance to report failure (Sarrazin & Barbault 1996). There may be a reluctance to perform robust tests which makes fundamental research difficult. The pheasant rearing and release system allows for many of these problems to be solved (See section 7.1.). The pheasant and partridge rearing system can act as a surrogate for many endangered galliformes, including the malleefowl, the rusty-margined guan, the dusky-legged guan, the greater-sage grouse, the sharp-tailed grouse, and the white tailed ptarmigan (WPA/IUCN 2009). It also allows for developing the field of rearing animals in an intensive environment for release into the wild.

I have shown that even in systems where captive rearing requires an absence of parents or informed conspecifics, the creation of a more naturalistic rearing environment can promote the development of important survival traits. Welfare is typically poor for animals kept in captivity for the purposes of translocation, even if only in captivity for short periods of time (Coddington & Cree 1995; Gregory *et al.* 1996; Nephew, Aaron & Romero 2005), therefore it is important to note that these naturalistic environmental manipulations did not compromise welfare.

I have also shown that personality can have important implications for a release programme beyond the shooting industry. Dispersal of shy and less social individuals from a release site would cause the population to skew towards bolder and more social individuals, opposite predictions to what was found by Madden and Whiteside (2014). Having population skew towards particular personality traits will have fitness consequences (Dingemanse & Réale 2005; McDougall *et al.* 2006; Smith & Blumstein 2008) and will not best prepare a population to have the behavioural and genetic variety to cope with fluctuating environments (Stamps & Swaisgood 2007).

I have highlighted the importance of screening personality types prior to release in order to determine individual fate and dispersal; ultimately allowing the researcher to determine the best release strategy to create a self-sustaining population. This can be achieved through determining the optimal group-dynamics for release (as suggested by Watters, Lema & Nevitt 2003; Watters & Meehan 2007) or the best release environment. (as suggested by Bremner-Harrison, Prodohl & Elwood 2004; Bremner-Harrison, Cypher & Harrison 2013).

7.4. Future directions

This study has highlighted key areas that, although compelling, require more research, either to test future hypotheses arisen out of the study or to refine some of the developmental process.

7.4.1. Manipulations to rearing environments

There are three important ways that this research can be forwarded. Firstly, there is an effort to refine manipulations to make them cost effective (Wallace 1994). Learning processes often have sensitive phases that allows for maximum learning, by provisioning specific stimuli during these phases it may improve the learning of that

particular trait and also reduce the time needed to provide the stimulus. For instance, the provision of insects during the first three weeks alone, analogous with forage consumed by wild chicks (Dalke 1937; Warner 1979), may results in the same learning as providing the same diet for 6 weeks as adopted in **Chapter two**, potentially halving the cost of the manipulation. In **Chapter three** I found that birds had increased propensity to roost at night if they had previous exposure to perches, but the effect of rearing treatment was nullified within 6 weeks post-release, indicating a form of social learning within the release pen. This can be refined by seeing how many "informed birds" who have learned to utilise perches are required to produce the same number of birds roosting at night within six weeks of their release. This could vastly reduce the cost of provisioning all houses on a rearing site with access to perches.

The second way to extend the research is to replicate all conditions subjected to pheasants mimicking commercial conditions. This study reared 900 pheasants in 30 houses at densities half of that experienced currently on game rearing facilities. Therefore the next step could be to increase the rearing density and gross numbers and see if the same effects are found. I feel that because much foraging is individually learned via trial and error I do not expect to find differences through having a higher density. However, higher densities are synonymous with increased aggression (Nicol *et al.* 1999), and adding a highly resource-rich stimuli may cause increased aggression, and result in some animals not obtaining suitable nutrients. Therefore finding ways to present the feed to reduce the risk of competition and aggression is necessary. Similar problems may arise with the provision of perching in intensive rearing conditions. It is possible that adopting a perching system in intensive rearing facilities may cause higher levels of mortality and bone malformation as a result of flocking and flying into the structures, as feared by (Gregory *et al.* 1990; Appleby, Smith & Hughes 1993). One simple way to ameliorate this is to position the perches around the edge of the pen such that birds are not flying at speed into them.

I released my 900 pheasants onto an estate which released a further 8000 birds each year. All the additional birds were reared in intensive and artificial conditions analogous to my control. Although I was able to compare across treatments, there may be density dependence for the post release survival. For example, predation typically accounts for around 25% of the released population and 'trained' birds reared with access to perches were less likely to be predated than control birds. The question here would be what would happen if all birds were 'trained' to avoid predators? Would predators have to still consume the same percentage, but simply having to work harder? In addition, for those with more adaptive foraging behaviour; if all released birds were capable of foraging in the wild what would happen? Would they rid the environment of natural resources and then be reliant on supplementary feed? The effects could be studied using two release sites where on one site only trained birds are released and on a second site only control birds release. These sites would have to be similar in environment and predator numbers.

A final way of forwarding the research is to concentrate on other characteristics that affect survival. Predation is the highest cause of mortality in pheasants (Robertson 1988; Brittas *et al.* 1992), and so by utilising conditioning work on predator avoidance through early exposure to predators and the demonstration of correct escape responses (Griffin, Blumstein & Evans 2000), which has had some success in released populations (van Heezik, Seddon & Maloney 1999), survival of released pheasants may be improved further. This could be achieved in a number of ways using the pheasant system. The first would be to return to the historical method of rearing with broody hens that have learned to fear predators, and then introduce the predatory stimulus during the rearing. This has been studied before, with much better survival for bids reared with informed conspecifics compared to hand reared birds (Buner & Schaub 2008; Ferretti *et al.* 2012), however the problem lies in the number of birds that can be reared under a broody hen compared to an artificial brooder. A second method would be to adopt the strategy used by Griffin, Evans and Blumstein (2001) on tammar

wallabies (*Macropus eugenii*) but on an industrial scale. Here a presentation of a model predator can be accompanied by conditioning fear by chasing the animals. I was unable to conduct such experiments for this study as I was limited by ethical and time considerations. Inducing fear into a captive rearing environment would compromise animal welfare and would require additions to the home office licence.

7.4.2. Welfare

It has been suggested that there is a trade-off between welfare and the production of survival characteristics (Rabin 2003) with some conditioning methods, such as the presentation of an adverse stimuli or a feeding method to increase competition leading to unacceptable levels of stress (Stahl & Kaumanns 2003). I feel that the effects of environmental manipulations aimed at preparing individuals for release into the wild needs closer examination. It is important to determine the threshold between stress levels that induces the learning of important survival trait and stress levels that are maladaptive to learning. This involves highly controlled conditions, would require home office licences and would be most effective if conducted using a system that allowed focused monitoring in both the rearing and post-release phase. This could be achieved by a highly focussed cognitive study where groups of pheasants are subjected to different levels of stress and then provided with a number of cognitive tasks to determine rates of learning.

I advocate all researchers conducting a release programme to monitor and report welfare. This work would allow the trade-off between pre-release welfare and post-release success to be analysed.

7.4.3. Personality

In **Chapter five**, I used return data collected from retrieved wing tags to determine the fate of birds released into the wild. To determine dispersal I used retrieval of wing tags from birds shot on and off the estate. Although crude, these

methods do provide an adequate form of dispersal and mortality data (Dickens *et al.* 2009). However, a more focused monitoring strategy using radio collars and trail cameras would help produce a stronger argument. A more precise measure of survival and movement would allow us to confirm our assumption that as the shooting season progresses and bold birds get shot, their density falls in the release area, and the shy and asocial birds that dispersed early in the season return.

Several suggestions for future work in the area of personality were suggested in **Chapter five** which may increase the success of released individuals in a release programme. Therefore I suggested a number of management manipulations that could help increase the success of a programme through the use of habitat management within the release site. I suggest that the creation of a release environment that accommodates animals with all personality types would allow for a founder population with the genetic and behavioural variances essential for creating a self-sustaining population. Clumping resources such as feeders, drinkers and shelter into a small area will promote competition and increase density. By spreading these resources and making them more numerous it will allow for asocial and shy birds to remain on site. The success of such a scheme could be assessed using pairs of release sites that are similar in environment but differ in distribution of resources. Pheasants can be personality tested prior to release and then allocated to one of the release sites, making sure that each release site contains the same number personality types. Following their use of the environment, survival, and dispersal will allow us to determine which site is best for the release of a diverse range of personality types. Because shooting can influence movements of birds with different personality traits (Madden & Whiteside 2014), it is best that this work is conducted on a release population not attached to shooting.

7.5. Why use a holistic approach?

There has been a strong impetus for science based research to help understand why differences in survival occur in release programmes (Armstrong & Seddon 2008). It is informative and indeed exciting to link the cognitive, behavioural and physiological mechanisms that impact a survival skill; however in typical conservation-focussed release programmes the constraints associated with release into the wild means that this is not always possible, and could be the reason why little research is conducted looking at mechanisms in concert with differences in survival of released animals. Section 1.5 highlights many of studies which looked at how reintroduction biologists have manipulated pre-release rearing environment in efforts to promote post release survival or post release behaviour, very few of these look at both. Survival is a product of multiple factors, and looking at them in isolation may miss out other crucial main effects or interactions. For instance, foraging behaviour is a result of a complex interplay between food discrimination, preference, handling, gut morphology and digestibility (Thomas 1987). The approach I used in this study is unusual in that it combines a whole range of factors likely impacting on a single pathway to improve survival. Including welfare in the holistic model allows the researcher to add an ethical standard to the work. Combining behavioural, physiological, cognitive development as well as welfare implications allows for a more powerful argument which may increase the likelihood of a manipulation being adopted.

7.6. Final summary

I have shown that the pheasant rearing system is ideal for studying the effects of manipulations to the rearing environment or for assessing the effects of personality on future success. This system allows for high release numbers, replicable conditions and a bird that is robust enough to take morphometric data and conduct behavioural tests. Therefore, I feel that future work in the fields of reintroduction biology,

behavioural and cognitive development and personality would all benefit using the pheasant rearing system as a model.

This thesis contributes to the growing field of reintroduction biology as it provides one of the first studies looking at manipulations to an intensive rearing programme. It also provides one of the first insights of how personality can affect dispersal and mortality in a high number release programme. Finally, this thesis highlights the need to use a holistic approach to understand multiple different factors leading to differences in survival and reproduction. By considering behaviour, physiology, cognition and welfare when rearing and releasing birds, I can be more confident in my findings (e.g. I obtain similar, concordant results across domains), understand the underlying mechanisms (e.g. how development influences physiology in tandem with cognition), and assess potentially conflicting outcomes in an industrial context (e.g. whether better surviving birds simply flee the release site). If my findings can be replicated in more industrial settings, then I can suggest low cost and non-labour intensive manipulations which can influence behavioural, physiological and cognitive development which improve post release survival resulting in environmental, ethical and economic benefits for both specifically the commercial game-shooting industry, and more generally projects involving captive breeding prior to release for conservation aims.

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